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MICHIGAN ACADEMY OF SCIENCE, ARTS AND LETTERS

VOLUME XI

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(This volume contains papers in Botany and Zoölogy only. Volume XII will contain papers in Anthropology, Economics and Sociology, Geography, Geology and Mineralogy, Language and Literature, Psychology, and Sanitary and Medical Science.)

PAPERS

OF THE

MICHIGAN ACADEMY OF SCIENCE ARTS AND LETTERS

EDITORS
EUGENE S. McCARTNEY
UNIVERSITY OF MICHIGAN
PETER OKKELBERG
UNIVERSITY OF MICHIGAN

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THE GENUS CALLIXYLON FROM THE UPPER DEVONIAN OF CENTRAL AND WESTERN NEW YORK

CHESTER ARTHUR ARNOLD

INTRODUCTION

ABOUT 1923 Dr. L. C. Petry commenced an investigation of the plant remains of the Devonian of Central New York. The author became associated with it in 1925 and this account embodies the results of the work of the three years following. In addition to material collected by Dr. Petry and the author, some material which had previously been collected by other individuals from the region under consideration was supplied by the New York State Museum. With one exception, all the localities from which material is described, either that collected during the course of the study or supplied from other sources, were visited and the condition of preservation and the nature of the strata were noted.

The author wishes to express his appreciation to Dr. L. C. Petry, under whose direction the work was pursued; to Miss Winifred Goldring of the New York State Museum; to Miss C. A. Black for her re-investigation of some previously described material; to the officials of the Redpath Museum of McGill University for permission to study some of their material; and to Dr. G. R. Wieland for his keen interest in the problem and the many helpful suggestions which he offered.

THE PLANT-BEARING HORIZONS

The localities within which the plant-bearing horizons were studied, with the exception of a locality in Erie County, are confined to a region in the west-central portion of New York extending in a northwest–southeast direction for about fifty miles. Material satisfactory for study came from the counties of Tompkins, Seneca, Yates, Ontario and Erie.

1. The Genesee Shale

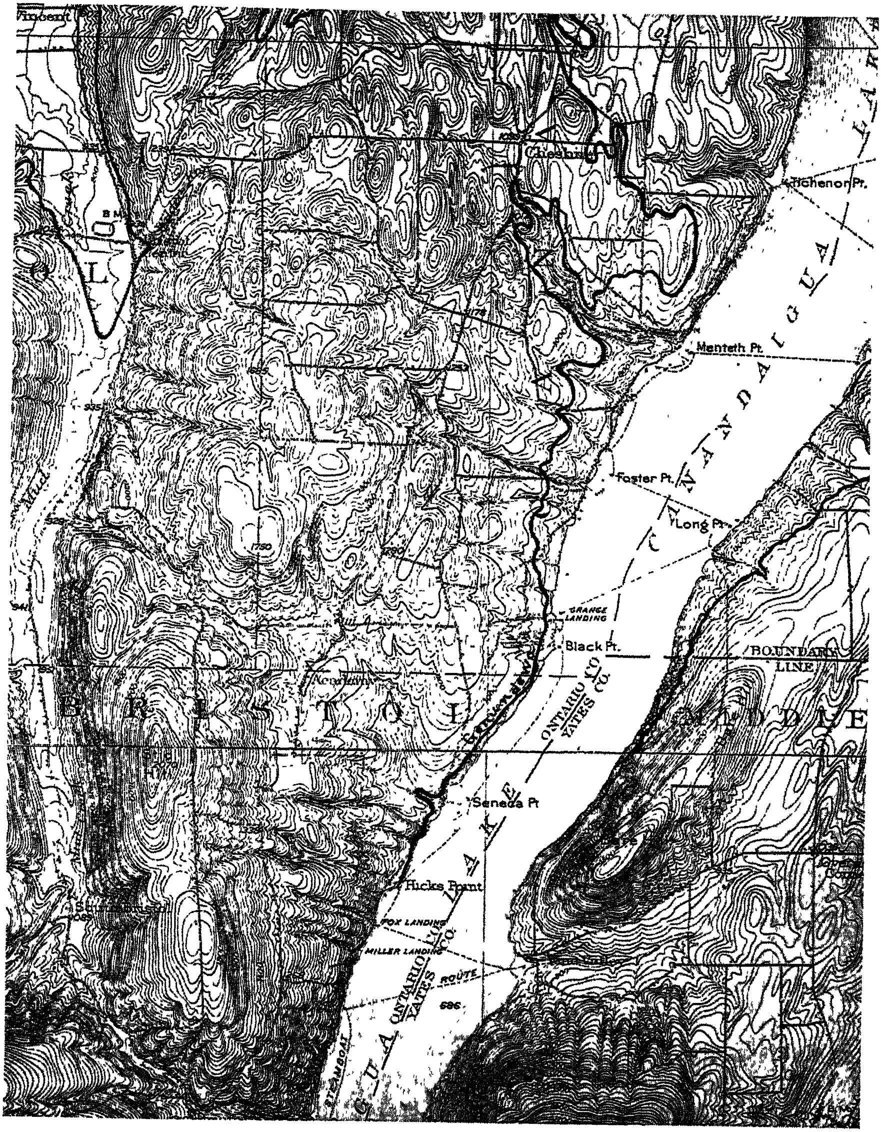
The lowest horizon in this region in which remains of Callixylon have been found is the Genesee shale. This shale is first mentioned by James Hall in the *New York Geological Survey, Annual Report*, 3 (1839): 301. At present the name is restricted to the densely black and bituminous beds, of a thickness of one hundred to two hundred feet, that lie between the Tully and the Genundewa limestone layers. Westward it diminishes to one foot in thickness on the shore of Lake Erie. It does not extend east of Smyrna, Chenango County (Luther, 20). A description of the formation, difficult to improve upon, is given by Luther (19):

> A homogeneous mass of densely black thinly laminated bituminous shale that after exposure becomes fissile and splits into flat plates. The beds are usually traversed by approximately parallel series of joint planes that intersect each other at different angles producing on the surface of horizontal exposures triangles, diamonds, rhomboids, and other kindred forms, and in cliffs striking effects like bastions and buttresses. In old exposures the outward angles have been worn away and there are left rounded masses of black shale partly covered in sheltered places by a thin white efflorescence of alum produced by the decomposition of the contained iron pyrite.

Petrified plant remains are exceedingly rare in this horizon and to date the only well-preserved specimens are from Seneca Point ravine on the west shore of Canandaigua Lake (Arnold, 1) and South Wales, Erie County. The large, hard, calcareous concretions, so abundant in the Genesee shale, were found to be relatively barren of plant remains.

2. The Genundewa Limestone

The principal plant-bearing horizon of the region under consideration is the Genundewa limestone which lies immediately over the Genesee shale. It is best developed in the vicinity of Canandaigua Lake (see Map 1) and was so named because of its



MAP 1. Portion of the Canandaigua and Naples quadrangles showing the Genundewa limestone horizon and the principal fossil plant localities. From *New York State Museum Bull.* 63 (1904), with modification

favorable exposure at Genundewa Point on the east shore (Luther, 19). Clarke (4) describes the Genundewa as follows:

> Wherever occurring this layer is quite unique in its composition, consisting almost wholly of the shells of the minute pteropod (*Styliolina fissurella*), which are so small that they measure no more than 1½ to 2 mm. in length, and so abundant that I have estimated from good specimens of the limestone at least forty thousand individuals to a cubic inch of the rock. . . . Thin sections show under the microscope that the rock has little else in it than these exuviae so closely crowded together that not infrequently one individual is thrust inside the other, and a third inside the second. In whatever direction of a fragment of a rock a thin slice is made, all the interspaces between the individuals which have been longitudinally cut are usually completely filled with transverse sections of other individuals, lying at varying angles to those which have happened to be longitudinally cut. Interspaces too small to accommodate a *Styliola* are very often filled with bituminous matter, and it is quite common to find in the interior filling of the *Styliola* a considerable intermixture of organic matter left from the decomposition of the original tenant of the shell. [See Pl. II, Fig. 1.]

In the vicinity of Canandaigua Lake the Genundewa horizon consists of three layers of rather soft and slightly shaly nodular limestone. Each layer is less than a foot thick. They are separated from one another by intervening bands of shale; the entire horizon has a depth of about fifteen feet.

The nodules of the lower layer are rounded and separate rapidly from the surrounding shale. In the two upper layers, where the plants are found, the nodules, instead of being rounded and distinct from the enclosing shale, are indefinite, with the bedding planes extending part of the way in and the surrounding shale grading into them. It is where a branch, twig or piece of secondary wood happens to pass through one of these nodules that the structure has been preserved. Of the ends of those plant structures which extend beyond the limestone cores into the shale, only a flattened oval mass remains.

The individual nodules of the upper layers vary in size from one inch to one foot in width, but they frequently run together and form a more or less continuous mass.

Some of the localities in which plant remains have been found along Canandaigua Lake have previously been reported (Arnold, 1). Subsequently the investigation has been extended to Bristol Center, a village about five miles west of Canandaigua

Lake. It was here that Clarke first observed the abundance of fossil wood in the Genundewa (Clarke, 4). At Bristol Center the limestone layer forms the crest of a small rapid in Wilder Run some two hundred yards northeast of the village. A single slab of the limestone about eight inches thick and six feet square yielded four or five specimens of well-preserved wood, including two stems with pith and primary wood preserved (Pl. I).

Along Seneca Lake the horizon has been studied at Lodi Glen and Fir Tree Point. Here the limestone is weakly developed and what wood fragments have been found were very poorly preserved.

Along Cayuga Lake the limestone with its characteristic Styliolina shells is absent, although the Genundewa horizon can still be recognized where the Genesee shale merges rather abruptly into the Portage immediately above. The horizon can be seen along the side of Taughannock Gorge and it may be examined more intimately in some of the smaller ravines directly across the lake from that point. In these ravines the horizon is marked by a layer of small, dark, calcareous concretions very similar to those of the Genesee, the extreme upper part of which they probably represent.

3. The Portage Group

The Portage group, which lies immediately above the Genundewa horizon, is relatively barren of preserved plants. The only material used in connection with the present study was discovered by the writer in 1926 on the Cornell University campus (Arnold, 1) and by Dr. Petry in Taughannock Gorge in 1924. The material collected by Dr. Petry was found in a rock fall on the north side of the creek about one hundred yards from the foot of the main falls. The exact level from which it came is, therefore, uncertain, but the presence of sandstone layers two or three inches thick immediately above the plant remains is sufficient to indicate the horizon as lower Portage instead of Genesee, as formerly reported by the writer (1). The material from the Cornell University campus was found in a local limestone pocket which had become exposed during excavation operations for the

Baker Dormitory site. So far, this locality is the highest in the geologic column of this region in which plants with preserved structure have been found, with the exception of a small amount of pyritized material from Fall Creek east of Ithaca.

In Taughannock Gorge the Portage formation consists mostly of the Cashaqua shale, but should probably include also the rather weakly defined West River horizon which separates the Cashaqua from the Genundewa. At Ithaca, on the other hand, the corresponding Portage horizon is classified by Williams (33) as Sherbrune, the lower 185 feet of strata above the Genundewa horizon, and the Ithaca, represented by the next 90 feet above. This difference in nomenclature is due partly to the fact that the two quadrangles which include the localities mentioned were surveyed by different individuals and partly to the different faunal relations present in the Portage to the west and in the Oneonta to the east (Barrell, 2).

The plant remains from the University campus came from the Ithaca shale, which will be considered along with the Cashaqua, since there is no distinction between the formations in the vicinity of Cayuga Lake.

THE PLANT REMAINS

The comparative rarity of plant fossils in the Genesee and Portage formations can be attributed to one or more of three possible conditions: first, there may have been very few vascular plants during the upper Devonian; second, the sediments may possibly have been laid down in an extensive sea far from plant-covered land masses; and, third, conditions may not have been favorable for preservation. A study of the Devonian sediments leads to the conclusion that the rarity of plant remains is due mostly to the last two conditions. The relative abundance of highly specialized plant structures in the Genundewa limestone is very satisfactory evidence that plants flourished in great abundance, but the fragmentary nature of the preserved parts, their decorticated condition, lack of attachment to anything resembling old soil, and the frequent association with them of marine fossils all indicate that the fossils represent drift material which floated for some time before becoming water-logged and buried. In this connection Clarke (4) is pertinent:

> The abundance of wood in certain places suggests close proximity to land, perhaps wooded islands, or the mouth of some large continental water course through whose agency the driftwood was carried out to sea. Its association, however, with Styliolina leads to the belief either that it must have been carried in large quantities far out to sea, or that the pteropods were swept in by ocean currents from deep water. The latter may be more probable, inasmuch as the character of the fauna and flora as a whole, with the lithological features of the formation, are such as to indicate a quiet, protected, and moderately shallow sea. The occurrence of the crinoid, *Melocrinus*, has a definite bearing on this conclusion.

There is additional evidence that the scarcity of preserved plant material in horizons other than the Genundewa is due to conditions which were unfavorable for preservation. In some of the formations, chiefly the Cashaqua, the sandstone masses are deeply mottled with flecks of dark material resembling pieces of macerated wood. They are suggestive of bacterial action upon partially buried plant tissues in which disintegration took place before petrifaction could occur, leaving only the fragments of the more resistant sclerenchymatous tissues. Such material is commonly observed in Taughannock Gorge and in the ravines about Ithaca.

The great quantities of bituminized wood in the upper Devonian rocks of this region is proof that plants flourished during that period, but in the absence of a preserving substance the plant tissues were reduced to coal-like masses with no cellulose structure remaining. Bituminized wood fragments are the most abundant of plant remains and the first to attract the attention of the casual observer. They are most frequently seen in sandstones, since the weathering of shale allows a rapid disintegration of such material. They occur as thin strips of coal-like material only a fraction of an inch thick. In the center and extending longitudinally through the flattened mass is often a thin strip of shale or sandstone. This strip, being surrounded by coal, represents the pith of the original stem. One such specimen from Taughannock Gorge (Pl. II, Fig. 2) measures 7½ inches long and 1¼ inches wide with a thickness of one eighth of an inch. The flattened pith core is three quarters of an inch wide and is surrounded by coal having a width of one quarter of an inch on either side, but consisting of a very thin layer above and below. The pith core is not transversely ribbed in the manner characteristic of Cordaites. Specimens as much as 10 inches in width and two or three feet long have been observed on sandstone slabs in Lodi Creek. The majority of them, however, range from an inch or two wide and a foot long down to a small fraction of an inch in either dimension.

Inspection of these bituminized remains shows no leaf scars or surface markings of any sort which can be utilized for identification. Like the petrified remains, they probably represent decorticated stems which drifted about, receiving all sorts of rough treatment before becoming water-logged and buried. The common occurrence of strips with coal on one side of the pith core and the other side in contact with the shale or sandstone, representing halves of stems, is suggestive of driftwood which has been subjected to alternate wetting and drying with consequent splitting. Several such specimens have been observed at Taughannock. These remains are probably stems of Callixylon, because of their frequent occurrence with Callixylon wood.

In fossil wood with structure preserved, the preservative, in the strata under consideration, is commonly calcium carbonate. Calcified wood occurs in all the localities referred to in the opening pages of this paper. In every case the structural fossils were completely surrounded by limestone which, with the exception of that in the Cornell locality, was nodular.

Preservation by iron sulfide (either pyrite or marcasite) is common in the Portage foundation and to some extent in the Genesee shale. In many specimens iron sulfide and calcium carbonate occur together, so that the cells which appear opaque in thin section are seen to be filled with the yellow iron sulfide crystals when examined by reflected light. The iron sulfide has a tendency to be deposited near the center of the stem and it is quite common to find the primary wood bundles badly pyritized and difficult to study, whereas the adjoining secondary wood is relatively clear.

A small amount of pyritized Callixylon material (some 12 numbers) was collected by Dr. Petry in the Ithaca shale (Cashaqua) along Fall Creek east of Ithaca.

PREVIOUS WORK ON DEVONIAN PLANTS OF CENTRAL NEW YORK

In 1885, when Clarke (4) first studied the Genundewa (Styliola) limestone horizon in Ontario County, he found associated with it numerous fragments of wood. He collected samples of it at Bristol Center and submitted them to Sir William Dawson, who described them as a new species, *Dadoxylon Clarkei.* Dawson's description, according to Clarke (4), was made from small pieces two or three inches in diameter, but Clarke said that he observed larger pieces at the same place.

The original description of *Dadoxylon Clarkei* is brief and without figures (Dawson, 10). It is described as having "a cellular pith surrounded by wood of coniferous type, showing two or three rows of slit-formed bordered pores in hexagonal borders. The medullary sheath consists of pseudoscalariform and reticulated fibers; but the most remarkable feature of this wood is the structure of the medullary rays, which are very frequent, but short and simple, sometimes having as few as four cells superimposed. — In any case this structure is new, and I have named the species *Dadoxylon Clarkei*, after its discoverer."

In 1889 Knowlton (18), in a revision of the genus Araucarioxylon, transfers *D. Clarkei* to Unger's genus Cordaites. He adds nothing new, but simply repeats the specific description given by Dawson. He refers to Cordaites all forms which possess the Artisia type of pith, but he gives no description of the pith of *D. Clarkei*, nor has a pith of the Artisia type been observed in any of the specimens labeled *D. Clarkei* which have recently been examined. It is difficult, therefore, to see what justification he had for referring this form to Cordaites other than the mere similarities in the structure of the secondary wood which, in this case, is without important distinctive characters.

A more satisfactory account of *Dadoxylon Clarkei* is given by Penhallow (22). He worked with type material which was submitted by Dawson and had some ten forms of Cordaites at hand for comparison. The first mention is here made of ray tracheids in this form and this character is used as the main distinguishing feature. Among other features he notes the well-developed pith composed of large, thin-walled cells, many of which contained starch. In a radial distance of fifteen millimeters there were, according to him, three vaguely defined growth rings in which the tracheids appear to have a somewhat shorter radial diameter. However, he considers them so poorly defined that the species agrees with the characters of the genus in the absence of well-defined growth rings. The bordered pits in the radial walls of the tracheids are in two to four rows throughout. The rays are quite variable in height, but are usually one cell wide, although they may be biseriate in part. The ray tracheids are long and narrow and interspersed, and bear numerous, crowded bordered pits on the upper and lower walls. He also says that some of these rays are comparatively broad and low, but their nature is uncertain from the rather obscure photomicrograph which accompanies the description. Mention is also made of the greater height of the ray tracheids in the higher rays. He failed to state whether the primary wood is endarch or mesarch and apparently considered the entire mass of primary xylem at the margin of the pith the protoxylem (Pl. IX, Fig. 2). The significance of this feature will be discussed in connection with the description of the genus Callixylon.

Both Knowlton and Penhallow mention the vagueness and inadequacies of the previous descriptions. In many respects their efforts have improved the situation, but the descriptions are still far from adequate and leave much to be desired. Knowlton merely quoted from previous authors in describing most of the genera and made no reference to type material. Penhallow (22) admirably summarizes the situation in the following words: "Looking at the various descriptions of the internal structure of the stem, one is immediately impressed with the inadequacy of the diagnoses and the too often loose and unscientific way in which the facts are stated, giving no adequate ground for comparison and the accurate differentiation of one species from another." Penhallow's description of *Dadoxylon Clarkei* is far more satisfactory than any previous work on that species, but the illustrations are insufficient and he had no idea of relationships or affinities of this wood.

The type material of *Dadoxylon Clarkei* was not examined during the course of the present study. It was originally deposited at McGill University, but our efforts to examine it have failed.

The name Cordaioxylon has been applied to some of the material collected by Clarke. Felix applied this name to the wood of Cordaites with the Artisia type of pith, but it has fallen into disuse and Cordaites is commonly used instead.

It is considered appropriate at this point to make brief mention of other plant remains previously reported from central New York. Probably the best known specimen is the "Naples tree," *Protolepidodendron primaevum,* from the Hatch shale in Grimes Gully one mile west of Naples (White, 31). This is an impression of a large tree trunk showing a combination of lepidodendroid and sigillarioid characters. It is now on exhibition in the New York State Museum at Albany. Penhallow (22) describes *Cordaites hamiltonense* from the Genesee shale of Ontario County. Until quite recently it was the only known specimen from this region with preserved bark, but otherwise it is poorly preserved and its exact affinity is uncertain. *Cordaites Halli* was discovered by Hall in Hemlock Creek, Ontario County (Penhallow, 22). It consists of a completely pyritized stem in which the structure can be studied only by reflected light; consequently little is known in detail concerning it. It was probably the first structurally preserved wood to be described from this region (Dawson, 8). A few other woods with preserved structure that are mentioned by Dawson (9) are *Celluloxylon primaevum,* collected by Clarke from the Hamilton group at Canandaigua; *Asteropteris noveboracensis,* a tree from the Portage at Milo; and *Dadoxylon mirabile,* also found by Clarke in the Genundewa limestone of Ontario County. Unfortunately the exact location from which these specimens came was not published.

Of impression material the "Naples tree" is the most important. There are also frequent references among the accounts by Dawson to imprints of various species of Lepidodendron, and occasionally to Calamites, Cyclostigma, Cordaites, Cyclopteris, Lycopodites and other genera.

The *Fucoides graphica* of the older literature is no longer considered a plant. Clarke (5) considers these markings on some of the sandstone slabs of the Cashaqua horizon to be imprints of spicular ice which formed in the loose sand. This interpretation has been criticized by Schuchert (24), who views them as fillings of worm holes. The specimen here illustrated was found in a stone fence on top of South Hill, Ithaca (Pl. III, Fig. 1).

THE GENUS CALLIXYLON

HISTORICAL

The genus Callixylon was founded by Zalessky (35) in 1911 on some material from the upper Devonian of the Donetz Basin, near the village of Bolchaia Karakouba, in south Russia. The type specimen was originally designated (Zalessky, 34) as *Dadoxylon Trifilievi* Zalessky, but a more detailed investigation of its anatomy convinced Zalessky that a new genus was indicated. He outlined the important anatomical features of this genus as follows:

(*a*) Mesarch primary wood bundles at the margin of the pith in contact with the secondary wood.

(*b*) Large irregular pith cells of which the length is several times the height.

(*c*) Pronounced anastomosing of the primary wood bundles.

(*d*) Narrow medullary rays.

(*e*) Divergence of secondary wood as it approaches the primary wood bundles to form wedge-shaped segments, and separation at these points by very wide rays.

(*f*) Arrangement of the pits in the radial walls of the tracheids into groups which are separated by spaces entirely free of pits.

The first and last of these characters are the most pronounced. The photomicrograph accompanying the description shows the pit groups to be radially aligned so as to present a characteristic cross-banding (Pl. IV, Fig. 1). This cross-banding is a feature hitherto undescribed in any fossil wood (except *Dadoxylon Newberryi*); from all the evidence at hand at present it is sufficient to distinguish a member of the genus. Of course, there still exists the possibility of discovering a form with this type of pitting, but with a different type of primary wood, in which case a new genus or possibly a new family could be established. At present the possibility of such a find seems improbable because hitherto only mesarch primary wood has been found with this type of secondary wood.

Callixylon Newberryi (Dawson) Elkins & Wieland was the first member of the genus to be described in America. This species was collected by Dr. J. S. Newberry from the Devonian of Ohio and was first described by Dawson (10) as *Dadoxylon Newberryi.* Dawson's figures and description of this form are very inadequate and he failed to record the grouped arrangement of the pits. Knowlton (18), in transferring it to the genus Cordaites, also overlooked this important fact, since he merely repeats Dawson's description. In the same year (1889) Newberry (21) made a more thorough diagnosis of this species and figured the grouped pits for the first time. Penhallow (22) uses the grouped pits for separating the species from other members of Cordaites, but otherwise he adds very little to Newberry's description. If the primary wood was present in the type specimen, its significance was not realized. Zalessky (35) mentions the similarity of the pit arrangement in this and the Russian species. In 1914 Elkins and Wieland (11) transferred this form to Callixylon.

The descriptions of *C. Newberryi* are vague and the figures crude. However, since we are largely dependent upon these for our knowledge of this species — the type has only recently been located — Penhallow's diagnosis is here quoted in full:

> *Transverse* — Tracheids 44 × 55 microns. Walls about 12.5 microns thick. In radial extent of 17 mm. no evidence of growth rings (obscure or obsolete). Tracheids conspicuously squarish sometimes unequal in the two diameters.
>
> *Radial* — Ray cells resinous and starch bearing, long and narrow, about equal to 3–7 tracheids, ends conspicuously narrower, the pits on the lateral walls 3–6, chiefly 4 per tracheid, the slit-like orifice nearly the full diameter of the pit. Bordered pits numerous, round, about 9.3 microns broad, distributed in radially disposed groups of about 10–13, the orifice diagonal and extending nearly the diameter of the pits.
>
> *Tangential* — Rays of medium height, 1–2, rarely 3-seriate in part, 24–55 microns broad, the oval or round cells all thin walled.

This diagnosis is accompanied by one photomicrograph of a radial section, but the area included is too small to serve as an adequate basis for comparison with other forms.

Callixylon Oweni Elkins & Wieland (1914) came from the Indiana Black Shale. Concerning its locality and horizon, Wieland (14) says:

> I noticed among some unstudied examples of silicified wood in the Yale collection a medium sized hand specimen from Lexington, Scott County, Indiana, which had evidently been acquired many years ago from Mr. J. H. Thompson of Hanover. Later, on inquiry, Dr. Edward M. Kindle, who is thoroughly familiar with the Indiana localities and stratigraphy, assured me that the specimen must certainly be from the Black Shales of the upper Indiana Devonian, which are approximately of the same age as the Genesee Shales of New York. He also stated that sections of trunks, a foot or more in diameter, had at various times been noted in the Black Shales.

The preservation in the specimen is good and in the hands of an expert technician some excellent sections were made. The secondary wood only is present and it was assigned to Callixylon solely on the grouping of the pits.

This species differs from *C. Newberryi* in several ways. The tracheids are slightly larger in *C. Oweni*, but hardly enough to constitute a specific difference. In a radial extent of 15 mm. six growth rings appear as opposed to none or very obscure rings in *C. Newberryi.* They are conspicuous on account of being filled with dark material, but it is uncertain whether this is resin or starch or other material deposited during silicification. The bordered pits are numerous, round or elliptical, in groups of 3–40, and in 1–4 vertical rows per tracheid. The groups of 40 pits are probably multiple groups. The hexagonal shape of the pits, which is due to crowding, is not so evident here as is common in other cordaitean forms. In tangential section the rays are 1–40 cells high, chiefly 1-seriate, sometimes partly 2-seriate, but never 3-seriate, all the ray cells are thin-walled, oval or round in section, and variable in size. The growth rings are somewhat questionable. They are obscure and, were it not for the curvature of the ring, it would be impossible to tell the inner from the outer face of the summer wood. Also there are interruptions in the course of the ring, so that the large-celled portion is often continuous with that of the adjacent ring. In addition, more or less isolated patches of cells resembling summer wood frequently occur which do not appear connected with any ring.

The third American species of Callixylon, *C. Marshii*, was collected from the Devonian of Eighteen Mile Creek, Erie County, New York, by O. C. Marsh in 1860, sectioned by Wieland in 1900, and described by C. J. Hylander (14) in 1922. The description is based upon a few sections of a small piece of very poorly preserved wood, but enough of the structure remains to show the radial grouping of the pits.

On account of the poor preservation, there is much doubt whether it is sufficiently understood to serve as a basis for comparison with other forms. The author states that the tracheids are consistently smaller than in *C. Oweni;* the groups contain fewer pits; and the rays are probably 2-seriate. Hylander's diagnosis is here given in full:

> Tracheids 35 × 45 microns in diameter, walls 3–5 microns thick, radial pits of the bordered cross-slit type, arranged in from one to three vertical rows of discontinuous groups of few to 12 or 13 pits to the group, groupings radially aligned; wood rays few to 20 cells deep, two cells wide, conspicuously broad in cross section; growth rings of primitive type present but difficult to see.

He claims that *C. Marshii* is closer to *C. Newberryi* than to *C. Oweni.*

Miss C. A. Black has recently reëxamined the sections of *C. Marshii* and she differs from Hylander in some respects. In a private communication she says:

> I find I differ from Mr. Hylander in three points: the width of the wood ray, the number of pits in the pit groups, and in the presence of a growth ring.
>
> In the text Hylander says (p. 319) the rays must be in part two cells wide. In his statement of the specific characters of *C. Marshii* (p. 320) he states that the wood ray is two cells wide and later in his comparison of *C. Marshii* with *C. Newberryi* and *C. Oweni* he says that they are at least two-seriate. I find the wood ray to be consistently one-seriate, only rarely finding it two-seriate. Certain of the wood ray cells have a peculiar marking, probably due to fossilization.
>
> Hylander gives 3–13 for the number of pits to the pit groups. I find a larger number, some running up to 18. I did not see any groups with fewer than 5. The state of preservation makes the smaller groups extremely difficult to count.
>
> In regard to the growth rings my conclusion is that the preservation does not permit a positive statement that growth rings occur. I can find places similar to Hylander's figure 5 where for a width of 6–8 cells there was an apparent ring of the discontinuous type, but in all such places there is a warping and compression which could also account for it.

Miss Black's reëxamination of *C. Marshii* indicates an affinity between this species and some of the other forms included in this study. The excellently prepared sketches (Pl. III, Fig. 2) which were submitted with the foregoing description show structures which are beyond all doubt ray tracheids; to these she refers as "a peculiar marking, possibly due to fossilization." She also mentions occasional biseriation, which holds true for our forms. Neither Miss Black nor Mr. Hylander gives an average of the number of pits per group, but she says that they range from 5 to 18, which is slightly low for our material, but the difference is not significant. The obscure nature of the growth ring is scarcely a diagnostic feature in such a poorly preserved form.

DESCRIPTION OF NEW SPECIES

Thin sections were made from twenty-four different specimens. Seventeen of these are mentioned in this paper and four new species are proposed. Of *Callixylon mentethense*, *C. erianum* and *C. bristolense*, only a single specimen is known. Several specimens are referred to *C. Zalesskyi*, with a single one designated as a type. Five specimens represent roots and are not given specific designation. The remaining seven specimens are placed tentatively with *C. Zalesskyi*, or are described separately and not given specific designation. The primary wood has been observed in *C. Zalesskyi*, *C. erianum*, and in several other specimens of uncertain specific identity.

Callixylon Zalesskyi, sp. nov.

Type. — No. 11074, Museum of Paleontology, University of Michigan

Transverse. — Tracheids 24 × 32 microns, somewhat variable in size and shape, but in general square to oblong. Ray tracheids abundant. Primary wood bundles 15–20. Pith 8–10 mm. in diameter.

Radial. — Bordered pits 10–24, averaging about 15 per group; in 2–3, rarely 4–5 vertical rows per tracheid. Ray cells about equal in height to cross-diameter of tracheids. Ray tracheids about equal in size and similar in shape to ray cells; length equal to cross-diameters of 2–5 tracheids; interspersed but frequently in rows for a distance.

Tangential. — Rays numerous, narrow, varying in height from 3 to 25 cells, but sometimes higher; partial biseriation common.

Distinguishing features. — Abundant, irregularly distributed ray tracheids which are similar in size and shape to ray cells.

Horizon. — Genundewa limestone.

The foregoing diagnosis was made from a type specimen from the falls of Menteth Brook one fourth of a mile south of the village of Cheshire, and another specimen from Seneca Point ravine. Since these two specimens seem to be identical in every respect, there is no hesitation in considering them conspecific.

The former specimen consisted of a complete woody cylinder measuring 15×30 mm. in diameter with a large pith surrounded by 5 mm. of secondary wood. The flattening is natural and was not caused by crushing. The pith is surrounded by 18–20 — poor preservation makes the exact number uncertain — mesarch primary wood bundles. These, with the radial alignment of the pit groups of the secondary wood, place this form without question in Zalessky's genus Callixylon.

The other specimen is very complete, but the preservation is poorer. It contains a greater thickness of secondary wood and the pith is more nearly circular instead of flat. Otherwise the two specimens are indistinguishable.

Another specimen which appears to agree in all essential points with the type specimen is one collected presumably by Clarke from the Genundewa limestone at Bristol Center in 1882. It was labeled *Dadoxylon Clarkei* Dawson and consisted of a slab from a long straight trunk which was probably 2 inches in diameter. The slab itself is about 1¼ inches broad and 2 feet long. The nodule within which it was contained is typical Genundewa limestone, consisting largely of the shells of Styliolina. The cut surface of the nodule and specimen had been polished and placed in the New York State Museum, where it had since been on exhibition.

Attached to this specimen and buried within the nodule was a small side branch about one half of an inch in diameter and a little more than an inch long. It departed from the main stem at an angle of 45 degrees. In the center is a small pith surrounded by several mesarch primary wood bundles. This character, along with the pit groups, indentifies it with Callixylon. Reference to other details of this specimen will be made under subsequent headings.

Callixylon erianum, sp. nov.

Type. — No. 11077, Museum of Paleontology, University of Michigan

Transverse. — Tracheids 35 × 36 microns, walls rather thick, square to round, regular in size and shape. Growth ring fairly well developed. Ray tracheids abundant and continuous for long distances. Pith large and surrounded by about 20 mesarch primary wood bundles.

Radial. — Bordered pits 1–16 averaging 6–8 per group, in 2, but sometimes 1 or 3 vertical rows. Ray tracheids conspicuous, in uninterrupted rows and of lesser height than the ray cells and alternating roughly with them, but sometimes 2 or 3 rows superimposed, length equal to cross-diameter of 2–4 tracheids, and walls vertical or slanting. Ray cells variable in size and shape, but in general higher than the ray tracheids.

Tangential. — Rays numerous and high, varying from 2 to 97 cells. Ray tracheids wider than high and ray cells higher than wide. Occasional ray tracheids divided by vertical wall, so that partial biseriation results, but without widening of ray.

Distinguishing feature. — Ray tracheids in uninterrupted rows which are distributed rather evenly among the rows of ray cells; very high narrow rays; fairly well developed growth rings; small number of pits per group.

Horizon. — Genesee shale.

This description was made from an excellent specimen collected by Dr. I. P. Bishop at South Wales, Erie County, in 1906. It was labeled "*Dadoxylon Clarkei*" and placed on exhibition in the New York State Museum. It consisted of a portion of a trunk about 6 inches long. The primary wood is in good condition, but the pith has been destroyed by lateral compression. The radially aligned pit groups and the mesarch primary wood identify it with

Callixylon, but it shows several characters which serve to distinguish it as a new species.

The appearance of the ray tracheids is striking. In radial section they are arranged in uninterrupted rows as far as they can be followed, and their tendency to alternate with the ray cells, as well as their uniformly lesser height, are characters peculiar to this form. This differs markedly from *C. Zalesskyi*, in which the rows are frequently interrupted, individuals often occurring singly, and not constantly of a lesser height than the ray cells. The difference is especially obvious in radial sections of the two species (Pl. V, Fig. 2; Pl. XIII, Figs. 2–3).

Because of the relatively great amount of secondary wood present the tracheids tend to be regular in size and shape. Their general shape is square to hexagonal or slightly rectangular, depending upon their arrangement one to the other. The secondary walls are thick, so that the lumina of the smaller cells appear round or oval. The lumina of the larger cells are more angular, but with the corners well rounded (Pl. XI, Fig. 2).

With the exception of two specimens to be described as "doubtful and uncertain forms," *Callixylon Zalesskyi* (Pl. V, Fig. 1) and *C. erianum* (Pl. XI, Fig. 1) constitute the forms with primary wood. They are especially significant in that in them we find for the first time the combination of mesarch primary wood and grouped pitting in American forms (Pl. XIII, Fig. 1). Concerning *C. Oweni* and *C. Newberryi* Seward (28, 3: 292) says:

> Miss Elkins and Dr. Wieland refer some Upper Devonian wood from Indiana characterized by a grouping of the circular or elliptical bordered pits in the radial walls of the tracheids similar to those in *Callixylon Trifilievi*, which they include together with the Middle Devonian species of *Cordaites Newberryi*, in Zalessky's genus. Though these two American species are comparable in the discontinuous arrangement of the tracheal pits with the Russian type, the latter is characterized by primary xylem strands, a feature not recognized in the American stems; it would seem, then, undesirable to adopt the designation Callixylon in preference to Dadoxylon unless there is evidence as to similar characteristics in the primary xylem.

Through a note in Hylander's paper (14), Wieland replied:

> It is not well to lay stress on the precise position in the middle or upper Devonian for any of these forms, since their time range is only inferable. The interesting and decisive point is that in middle or later Devonian time there

was a cosmopolitan group of Cordaites with grouped pits, and such forms are known in a typical instance to have cryptogamic wood. The probability is that all have it. But if any of the species referred to Callixylon, with reservations well within the recognized usages of Paleobotany, were later found to lack cryptogamic wood, then a new genus would be indicated, perhaps a new family. Moreover, mere reference to Dadoxylon would settle nothing, where these recurrently variant forms are concerned. With or without cryptogamic wood, there would still remain the chance that the leaf or floral characters varied strongly from the forms primarily designated as Dadoxylon. Like so many genera of Paleobotany, *Dadoxylon* is now more of a group name than a genus in the pure botanical sense. And similarly *Callixylon,* in the first instance a needed generic distinction, must share the same fate of ultimate and convenient inclusiveness.

The primary wood of *Callixylon Zalesskyi* and *C. erianum,* therefore, give Wieland further justification for referring the Indiana specimen to Callixylon. The specimens referred to these two species, together with the specimens of uncertain specific identity with mesarch primary wood, make a total of seven in which this character has been observed in association with the grouping of the pits. Of course there still remains the possibility of a different type of primary wood in some of these forms in which it is as yet unknown, but such a discovery seems increasingly improbable. At any rate such an abundance in this region of wood with such a distinctive character as the radial grouped pits, either with or without mesarch primary wood, indicates a group distinct from the typical Dadoxylon complex, the members of which are not common in the Genesee and Genundewa horizons in this region.

Callixylon bristolense, sp. nov.

Type. — No. 11078, Museum of Paleontology, University of Michigan

Transverse. — Tracheids small, 25 × 28 microns, square to roundish, thin-walled (Pl. XIV, Fig. 1). Growth rings absent or very obscure. Ray tracheids abundant toward center.

Radial. — Bordered pits 5–19, averaging 11 or 12 per group, in 2–3 rarely 3–4 vertical rows per tracheid, hexagonal and crowded. Pit orifice a vertical slit, the two opposing ones nearly coinciding. Ray tracheids scattered. Ray cells about equal in height to the cross-diameter of the tracheids, sometimes narrowed toward the ends.

Tangential. — Rays 19–47 microns broad, averaging 28 microns, variable in size and shape, from 3 to 20 cells high, the smaller ones pointed above and below, the higher ones more rounded, uniseriate with possible exception of the broadest ones.

Distinguishing features. — Vertical pit orifice.

Horizon. — Genundewa limestone.

The specimen from which this description was made was found in a fallen rock along the water's edge on the west shore of Canandaigua Lake north of Seneca Point. The Styliolina shells in the inclosing rock identify it with the Genundewa limestone, which is probably situated high on the cliff at this point. The specimen, which is about one inch in diameter, is a sector of a larger trunk, and though the primary wood is missing there are some indications, to judge from the appearance of the tissue nearest the original center, that this specimen may be a root. The diagonal pit orifice in material known to be roots shows that the vertical orifice is not peculiar to them.

The vertical pit orifice (Pl. XIV, Fig. 4) appears to be a character heretofore undescribed for any wood of Dadoxylon affinities. Such structures occur in the summer wood of *Pinus Strobus* and in the wood fibers of some angiosperms, but in these the cells are narrow with the pits in a single row. Though probably 90 per cent of the pits of this specimen have a vertical orifice, this condition is not universal. Scattered here and there are occasional pits or groups of pits with diagonal orifice in which the two opposing slits give the cross appearance. The predominance of the vertical type of orifice is sufficient, however, to denote specific variation.

Callixylon mentethense, sp. nov.

Type. — No. 11079, Museum of Paleontology, University of Michigan

Transverse. — Tracheids 36 × 37 microns, square to hexagonal or round, variable in size. Growth rings obscure. Ray tracheids scattered. Rays wide.

Radial. — Bordered pits 6–15 per group, averaging 11, mostly in 2–3 vertical rows, hexagonal and crowded. Ray cells about equal in diameter to the tracheids, length about equal to 3–5 tracheids, ends square, regular in size and shape. Ray tracheids scattered, irregular in size, frequently narrow at the ends, often containing resin-like material.

Tangential. — Rays variable, 6–20 cells high and 23–78 microns broad, averaging 48 microns, rounded at top and bottom giving oval aspect to smaller ones, frequently biseriate wholly or in part.

Distinguishing feature. — Broad biseriate rays conspicuously rounded above and below.

Locality and horizon. — Genundewa limestone at Menteth Brook ravine south of Cheshire, New York.

The specimen from which this description was made was a piece of well-preserved secondary wood measuring about one inch in diameter, but not including the pith. Except for the structure of the rays this form closely resembles *C. Zalesskyi.*

In transverse section the rays are generally wider than the adjacent rows of tracheids, though in most other forms they are approximately of equal width. In tangential section the rays are conspicuously broad, and owing to the rounded upper and lower extremities the smaller ones appear oval (Pl. XV, Figs. 1–2). The cell walls have disappeared in most specimens, but where they remain about one half of the rays are entirely biseriate. Some of the remaining rays are biseriate only in part and the others are wholly uniseriate. Instead of the biseriation consisting merely of 2 small cells placed side by side as in *C. erianum,* it is made up usually of alternately arranged cells which have 3 or 5 sides (Pl. XV, Fig. 2). A biseriate ray may contain a ray tracheid on one side and thin-walled cells directly across.

This species bears some resemblance to *C. Newberryi* which is described (Newberry, 21) as having biseriate rays. No mention is made of ray tracheids in *C. Newberryi;* until a more thorough study is made of the type of this species, it is unwise at present to consider the two as conspecific.

SOME DOUBTFUL AND UNCERTAIN FORMS

In the material studied are several specimens, which, either because of poor preservation or incompleteness, cannot be placed with certainty in any of the foregoing species. On the other hand it seems unwise to multiply species on the basis of differences shown by poorly preserved or otherwise inadequate material.

For convenience in reference these forms will be briefly described and designated according to their catalog numbers in the Museum of Paleontology of the University of Michigan.

Callixylon sp., No. 11080.

This specimen consisted of a poorly preserved stem portion measuring about 10 × 25 mm. It was found in association with several root fragments in a localized limestone bed in the Ithaca shale on the Cornell University campus. The tracheids are small, 23 × 30 microns, and the pith is 4 mm. in diameter. The primary xylem points, of which there are about 9, are poorly preserved, but the mesarch condition is visible. A feature of interest is the continuous pitting in some of the tracheids, the grouping not being universal (Pl. XIII, Fig. 4).

Callixylon sp., No. 11081.

Another specimen, very similar to the preceding one, is from the Genundewa limestone. It was on exhibition in the New York State Museum and bore the label *Dadoxylon Clarkei.* It differs from No. 11080 in showing a better development of the pit groups. It is also better preserved and resembles *C. Zalesskyi* except for the extreme rarity of ray tracheids. Whether or not they are absent could not be determined. A feature of interest in the latter specimen is the presence of medullary tracheids, structures which also occur in *C. Zalesskyi.*

Callixylon sp., No. 11802

The specimens from which this description is made were collected at the foot of Bare Hill on the east side of Canandaigua Lake. The characteristic feature is the large pit groups. Instead of containing about 15–20 pits, the general average in other forms, they run very high, averaging about 30 (Pl. XIV, Fig. 5). Many groups, which probably represent multiple groups, contain 100 or more. Some of the tracheids show continuous pitting. Ray tracheids are very rare in this form. The primary wood is unknown.

Callixylon sp., No. 11083

This form, from the Genundewa limestone at Seneca Point, is characterized by the presence in great numbers of very small rays (Pl. XIV, Fig. 6). Instead of being high, as in most forms, they run from 3 to 12 cells, the majority being not over 10. In some places throughout a section, however, there are areas with rays somewhat higher; hence the hesitation in describing it as a new species. The tracheids are very small, measuring but 19 × 29 microns. The ray tracheids are very abundant and continuous for long distances. In these latter respects it closely resembles *C. bristolense*, but the pit orifice is diagonal instead of vertical, so that at the present time the two forms cannot be considered conspecific.

Callixylon sp., No. 11084

A badly crushed and poorly preserved specimen was found in a limestone concretion in the Genesee shale just below the falls in Seneca Point ravine (Arnold, 1) near the place where one of the specimens of *C. Zalesskyi* was found. It consisted of a trunk measuring about 1¼ × 2 inches in diameter and 18 inches long. The flattening caused a complete destruction of the pith and crushing of the rays and tracheids in many places. This crushing and buckling was more pronounced toward the center where the wood was also badly cracked, rendering the number of primary bundles uncertain, but there appear to have been from 15 to 20.

Though the poor preservation has obscured many of the details, this specimen seems to correspond in a general way with the type specimen of *C. Zalesskyi*. There is a greater thickness of secondary wood (as in the specimen from South Bristol), which may or may not be significant. The number of pits per group runs as high as 40, but they average about 15. The wood rays are quite variable, many of them are small, but some are high and always narrow. They are badly crushed, however, and impossible of critical determination. The ray tracheids, although of uncertain abundance, seem to be of approximately the same diameter as the ray cells. Obscure growth rings are present.

Callixylon sp., No. 11085.

Another specimen from the Genundewa limestone at the foot of Bare Hill on the east side of Canandaigua Lake will be discussed at this point. It was found in a nodule lying at the water's edge and consisted of a piece of secondary wood about an inch in diameter.

It is quite variable in structure and differs from *C. Zalesskyi* in an almost complete absence of anything resembling growth rings and in the scarcity of ray tracheids. The ray tracheids which are present closely resemble those of the type. The variation in the size and shape of the rays presents the greatest difficulty in classifying it. They consist of three types: the high, narrow, uniseriate type which is typical of *C. Zalesskyi;* a low narrow type only a few cells high; and a broad, oval, biseriate type similar to that of *C. mentethense.* The first type predominates, but there is quite a gradation among all three. Rays of the broad type are not abundant, but they occur in certain areas throughout a section. The possibility that lateral compression might broaden some of the rays and thereby present a deceptive appearance must be taken into consideration, but there is no evidence of such flattening in this specimen, since there is no similar distortion of the tracheids. The rounded upper and lower extremities of the rays is, therefore, a normal condition.

Dadoxylon Clarkei Dawson

The specimen of *C. Zalesskyi* from the Genundewa limestone at Bristol Center, bearing the label "*Dadoxylon Clarkei* Dn.," has brought up the question whether the original *D. Clarkei* might be a Callixylon. Penhallow (22) gives the following diagnosis of *D. Clarkei:*

> *Transverse*—Growth rings obscure or wanting. The tracheids about 41 × 49 microns broad, walls 12.5 microns thick.
>
> *Radial*—Bordered pits numerous throughout the tracheids, in 2–3 rows, more rarely 4 rows. The elements of the medullary rays of 2 kinds; the paren-

chyma cells thin walled and devoid of pits, about equal to 3 tracheids; the ray tracheids long, interspersed, and bearing on their lateral and upper and lower walls numerous, crowded, bordered pits.

Tangential — Rays variable, commonly 1-seriate, but sometimes 2-seriate in part, the tracheids usually distinguished by their narrow form and pitted walls.

Clarke says (4) that the original description was made from some small specimens which were collected from the Styliola (Genundewa) limestone at Bristol Center. He also says that the wood was abundant at that place.

The Bristol Center specimen agrees well with the foregoing diagnosis with respect to the character of the rays and the ray tracheids. The measurements of the tracheids do not check so closely. Penhallow (22) says that the tracheids of *D. Clarkei* measure 41 × 49 microns. In a small transverse section which was loaned by the State Museum to Dr. Petry they measure 29 × 37 microns; in the Bristol Center specimen, 23 × 33 microns. Each of these determinations is probably from a different specimen, and there is no proof that they all belong to the same species or even to the same genus.

The difficulty is that none of the descriptions of *D. Clarkei* make any mention of radially aligned pit groups or of mesarch structure in the primary wood. Penhallow says that the pits are in 2–4 vertical rows per tracheid. He must, therefore, have had sections showing this character and the grouped arrangement was either absent or, if it was present, was overlooked. There is of course the possibility that his radial sections were poor or obliquely cut, in which case pit grouping might have escaped notice. One of his photomicrographs shows *D. Clarkei* with pith and primary wood (Pl. IX, Fig. 2). Although the protoxylem is visible in the picture, it cannot, because of poor preservation, be definitely identified as mesarch. He labels as protoxylem that region just outside and also between the true primary wood bundles which, in a Callixylon, would be the first-formed secondary xylem. The similarity of the situation in this figure to recently collected material, however, leaves little doubt but that the primary wood in Penhallow's specimen is mesarch.

From the material at hand it seems that *Dadoxylon Clarkei* was the name applied to almost any fossil wood specimen found in the New York Devonian and especially from the Genundewa horizon. A single transverse section through a stem two inches in diameter and labeled "*Dadoxylon Clarkei*" was also found in the State Museum. This section, while rather poorly preserved, nevertheless shows several mesarch primary wood bundles surrounding the pith. We know nothing of the source of this specimen other than the data on the label, which says, "Styliola layer, Bristol, N. Y." It might have been one of the original specimens collected by Clarke, but whether or not it is from a type specimen there is no known method of determining. Some material apparently was named without first being sectioned. For example, *Callixylon erianum*, which was labeled "*D. Clarkei*," consisted of a solid trunk two inches in diameter and about six inches long, which had not been cut into, not could any sections be located which might have been prepared from broken fragments.

Although it is possible that *Dadoxylon Clarkei* is a Callixylon, and all available evidence (except Penhallow's description) favors the assumption that it had mesarch primary wood and radially aligned pit groups, still it would be unwise to transfer it to Callixylon without first referring to type material, which is not available.

ANATOMY

The Primary Wood

1. *The primary wood bundles*

As Zalessky stated in the original description of the genus, the primary wood is mesarch and in contact with the secondary wood. A few scattered parenchyma cells may intervene, but they never completely separate the primary wood from the secondary tissues.

The number of primary wood bundles is variable. There are 9 in some of the smaller stems which may represent small branches, 18–20 in the Cheshire and Seneca Point specimens of *C. Zalesskyi* and about 20–24 in *C. erianum*. These bundles anastomose freely, as shown by the double bundles (Zalessky, 35), thereby forming a network surrounding the pith. Before the exact situation was understood it was suggested that these bundles represented double leaf traces (Seward, 28, p. 291), but the traces are single and not related to these double bundles in any way.

In that portion of a bundle undisturbed by an outgoing trace, the protoxylem is located not centrally but slightly toward the inside. The inner portion of the metaxylem is usually 2–4 cells in extent.

The primary wood of this genus shows a complete gradation from the annular, through the spiral, scalariform and reticulate tracheid. Seward (28) says of *Callixylon Trifilievi* that "the primary xylem shows particularly well transitional forms of pitting connecting the multiseriate and scalariform types." Nothing is said concerning the width of this zone nor the extent of each type.

In the type specimen of *C. Zalesskyi* the transition in a bundle undisturbed by an outgoing trace occupies about 7 cells in the following order: 1 narrow spiral (Pl. XVI, Fig. 2), 3 wide spiral-scalariform (Pl. XVI, Fig. 3) and 2 or 3 reticulate-pitted (Pl. XVI, Fig. 4). At another place in the same specimen the following succession could be determined: a narrow spiral cell, a parenchyma cell, a spiral-reticulate or scalariform cell, and a reticulate-pitted cell (Pl. XVI, Fig. 5). In this specimen it was impossible to observe the entire transition because of poor preservation in the protoxylem region of the bundle.

It is also appropriate at this point to remark on the difficulty of distinguishing between the various stages of the transition in fossil wood. The situation is particularly likely to be uncertain between the spiral and scalariform and reticulate elements. A decayed reticulate cell will probably appear scalariform and a scalariform cell will appear spiral, owing to the disappearance of the connecting bars (Pl. XVI, Fig. 6).

The transition is clearly shown in *C. erianum;* its excellent preservation permits the entire series to be studied. The very small protoxylem elements contain rather distantly placed rings which evidently represent the annular thickenings (Pl. XVII, Fig. 2). Beyond this the tracheids show the two vertical rows of horizontally elongated openings which should probably be referred to as reticulate rather than scalariform. Definite scalariform structure is probably not clearly marked. Following this are generally two or three tracheids with continuous pitting of the Dadoxylon type, and after these are the tracheids with grouped pits.

Whether these few tracheids with continuous pitting belong to the primary or the secondary wood, has not been finally determined. The radial arrangement of the tracheids between the primary wood bundles indicates that the secondary wood extends entirely to the pith at these places. Although it is difficult to obtain thin sections showing this feature satisfactorily, there seems to be some continuous pitting in the tracheids near the pith. The radial banding has been observed to extend to within two or three tracheids of the pith, but in no specimen yet observed can it be said to extend the full distance. One is justified, therefore, in assuming that the continuously pitted tracheids outside the reticulated ones belong to the secondary wood, the boundary thus being between the two types.

If the first-formed secondary tracheids show continuous pitting, the grouped pitting indicates a specialized character. Continuous pitting is probably the retention of an ancient character, indicating the derivation of Callixylon from the Dadoxylon or Cordaites stock.

The metaxylem between the pith and the protoxylem is mostly spiral, but it may become scalariform or reticulate, depending upon its extent.

This transition zone from annular to pitted structure is relatively brief for such an ancient form. *Dadoxylon Pedroi,* from the upper Carboniferous of Brazil, has endarch primary wood and a transition zone of about 12 cells (Pl. XVI, Fig. 1). *D. indicum* (Holden, 13) has a zone of 15 to 20 cells. In *Cordaites Brandlingii* (Scott, 25, p. 274) the zone occupies about 30 cells.

The significance of this brief transition zone is discussed later.

2. *Form and departure of the traces*

Some of the essential features of the departure of the leaf traces are shown in the Cheshire and Seneca Point specimens of *C. Zalesskyi* and in *C. erianum.*

A series of transverse sections shows that the origin of a trace from a circum-medullary bundle is initiated by a slight increase in the size of the bundle (Pl. VI, Fig. 1). At a slightly higher level the protoxylem divides and the two masses lie in a radial plane (Pl. VI, Fig. 2). Still higher the bundle divides, the space between the two being filled with parenchyma (Pl. VII, Fig. 1; Pl. XII, Fig. 2). As the trace works outward and away from the reparatory strand the parenchyma-filled space lengthens correspondingly, and later the secondary wood commences to close in just outside the reparatory strand, thus separating it from the parenchyma-filled area (Pl. VII, Fig. 2).

Since the reparatory strand continues uninterrupted at the margin of the pith from the point of departure of the trace, there is no true leaf gap. Longitudinal sections through the region of a departing trace support this interpretation (Pl. XII, Fig. 1). A condition similar to this has also been noted in *Calamopitys americana* and in *Archeopitys Eastmanii* (Scott, 25).

The angle of departure of the trace varies in different species. In *C. Zalesskyi* the trace, soon after leaving the reparatory strand, bends sharply outward and passes through the secondary wood at an angle of about 60 degrees from the vertical. In *C. erianum* it rises at an angle of 15 degrees from the vertical and continues thus for some distance before it commences to bend outward (Pl. XII, Fig. 1). Its course could not be traced for more than one centimeter in the specimen at hand.

A transverse section through the stem of *C. Zalesskyi* shows 5 to 7 traces in various stages of departure from the primary region (Pl. XVIII, Fig. 2). In a vertical distance of about 15 millimeters 4 new traces were found to originate. Of a total of 9 traces in various stages of departure in that length of stem no 2 are vertically aligned, so the phyllotaxy was probably high, $\frac{8}{21}$ or more.

The method of departure of the trace in *C. erianum* is the same as in *C. Zalesskyi*, with the exception of the angle of departure as noted above. No idea of the phyllotaxy could be obtained in this species from the material at hand.

The trace is mesarch in both species as far outward as it can be followed. The amount of metaxylem is greater than in the circum-medullary bundle below the point of origin of the trace, and in

C. Zalesskyi it is surrounded by a considerable thickness of secondary wood which appears to have resulted from a cambium surrounding the trace (Pl. VIII, Fig. 3).

There is no evidence of division of the trace in its passage through the wood, so that the probability is that it remains single into the base of the leaf. The apparent lobing which is discernible at certain places is more probably due to its attachment to the adjacent secondary wood rather than to doubling, since no division of the protoxylem can be detected.

3. *Medullary tracheids*

A feature heretofore undescribed for any member of this genus is the occurrence of tracheids in the pith. They occur in *C. Zalesskyi*, in No. 11081, and probably in other species also. They are for the most part isolated and scattered, but frequently occur in groups of as many as 4 or 5 (Pl. VIII, Fig. 1). Longitudinally they form a rather broken series which may extend for some distance up and down the pith. They are distinguished from the pith cells by being longer and narrower and by the spiral and scalariform secondary thickenings (Pl. VIII, Fig. 2). There is no apparent connection between these pith tracheids and the primary wood bundles.

The Secondary Wood

1. *The bordered pits*

The number of rows of pits per tracheid is determined by the size of the lumen. Most stems have 2 or 3 rows, but in roots in which the cells are larger they are commonly in 3 or 4 and occasionally 5 rows. A single row is common in the narrowest tracheids of *C. erianum*.

Continuous pitting, typical of Dadoxylon, was mentioned during the discussion of the primary wood. It occurs to some extent in the secondary wood of some forms. In No. 11082 the groups contain from 12 to 50 pits and occasional ones have from 75 to 100. (Pl. XIV, Fig. 5). Similar groups in *C. Oweni* have been considered as multiple groups (Elkins and Wieland, 11). Some of the tracheids in this form show no grouping at all. This condition was first noticed in

No. 11080 (Arnold, 1) in which many of the tracheids show continuous pitting. Another feature in this form is the extent of the unpitted areas between some of the pit groups (Pl. XIII, Fig. 4). Some of these are 2 to 4 times as long as the cross-diameter of the tracheids in which they occur. Others are quite short, having only an extent equal to the width of a row of pits. As far as the poor preservation of the specimen reveals the actual condition, the continuous pitting is not confined to any particular region of the stem.

Grouped pits have also been reported by Seward and Walton (29) in *Dadoxylon Bakeri* and by Miss Holden (13) in *D. bengalense*. *D. Bakeri*, from the Permo-Carboniferous of East Falkland, has either alternate or opposite pits, which are sometimes in stellate groups. These groups lack, however, the extensive distribution which is so characteristic of Callixylon. *D. bengalense*, from the Permo-Carboniferous of India, has groups of 2–5 pits each. These groups are not radially aligned, and since the primary wood of this form is unknown, Miss Holden does not consider this type of pit grouping sufficient to identify it as Callixylon.

2. *The wood rays*

In the original description Zalessky (35) says that Callixylon differs from *Pitys antiqua*, and resembles *Eristophyton fasciculare* and *Parapitys Spenceri* in having narrow rays. Since the tangential surface of *C. Trifilievi* is not figured, it is impossible to determine whether or not any biseriation is present in this form.

The material of Callixylon at hand shows considerable biseriation, as do *C. Oweni* and *C. Newberryi*. There is evidently some biseriation in *C. Marshii*, according to Miss Black's figures (Pl. III, Fig. 2). The rays of *C. Oweni* are uniseriate, but some are partially biseriate. Where such biseriation occurs there is a distinct broadening of the ray. A similar type of biseriation is exhibited in modern sequoias (Pl. XIV, Fig. 3). The published figures of the rays of *C. Newberryi* are unsatisfactory, but Penhallow (22) says that the rays are of medium height, 1–2-, rarely, 3-seriate in part; from 24 to 55 microns wide, and the oval or round cells of the ray are thin-walled. According to Newberry's figures (21) and a recent examination of the type material, the biseriate rays are broad and oval; the biseriation, at least in some cases, extends the entire height of the ray (Pl. XV, Fig. 3). This condition is very similar to certain broad, oval, biseriate rays in *C. mentethense* (Pl. XV, Figs. 1–2), in which it seems to be constant throughout and seems to indicate specific separation. In other specimens such rays appear sporadically or they may be congregated into more or less clearly defined areas. Wherever they do occur, they offer a marked contrast to the very high, narrow, uniseriate ray which is predominant in *C. erianum* and *C. Zalesskyi.*

Partially biseriated rays are common in *C. erianum.* They are produced by two narrow cells lying side by side; the two together are no broader than a single cell of the uniseriate portion (Pl. X, Fig. 2).

The biseriate condition is more variable in the different forms of *C. Zalesskyi.* In the specimen from Bristol Center the condition may be very similar to that of *C. erianum* or there may be certain rays which are biseriate for a considerable height, and rarely for the entire height of the ray (Pl. IV, Fig. 2). These rays, however, are much higher than the broad, oval, biseriate rays of *C. mentethense* or *C. Newberryi.*

The height of the ray, although showing some differences in various forms, can hardly be employed for specific separation. The rays of *C. erianum* are probably the most variable in this respect, since some of them have been found to be 97 cells high. The range is from 2 or 3 cells upward. In the majority of forms they seldom exceed 30 to 40 cells and rays with 10 to 20 cells are most common.

3. *Ray tracheids*

Ray tracheids are not mentioned in previous descriptions of Callixylon. Both *C. Oweni* and *C. Newberryi* are described as having ray cells with thin walls. Ray tracheids must be present in *C. Marshii,* according to Miss Black's figures (Pl. III, Fig. 2). However, this species closely resembles, and may be identical with, *C. Zalesskyi.*

Penhallow (22) mentions ray tracheids in his description of *Dadoxylon Clarkei* and says that they serve to distinguish this form beyond all doubt. He even suggests that they might indicate a new family. Observations on Callixylon during the course of the present study show, however, that their presence is not a family or even a generic character.

Ray tracheids are distinguished in transverse section by the pitting in the upper and the lower walls (Pl. IV, Fig. 3; Pl. XI, Fig. 2). These pits are in 1 or 2 (sometimes 3) rows, alternate, and closely crowded, so that when the preservation is poor the entire structure may have disappeared.

The distribution and arrangement of the ray tracheids within the ray have some specific significance, as is pointed out under the specific descriptions. In no form are they definitely known to be absent, but in some forms they are rare and scattered. In the forms which have them in abundance they are never limited to the margin of the ray, as in modern gymnosperms, but are distributed throughout the entire vertical distance. In *C. erianum* the ray tracheids cells are in radial rows and show a very regular distribution with reference to the ray cells (Pl. XIII, Figs. 2–3), while in *C. Zalesskyi* they are more scattered, in interrupted rows, and frequently with individual ray tracheid cells completely isolated from all others (Pl. V, Fig. 2).

The absence of ray tracheids in Araucaria and Cordaites has led certain investigators to question their presence in *Dadoxylon Clarkei*, as described by Penhallow (22). Thomson says (30):

> The medullary ray cells are characteristically thin walled in the Araucarians, and are comparable to those in the Cordaitean forms. They are unpitted in the Araucarineae as in the latter. Often these cells have been wrongly spoken of as having pits in the lateral walls where they come in contact with the tracheids, some anatomists even going so far as to distinguish the pitting as of the bordered type. Gothan has noted this especially in the case of Penhallow when discussing Penhallow's statement that there are ray tracheids in *Cordaites Clarkei*. He says that all Penhallow's ray cells are tracheids on account of their pitting. With this as a basis and the fact that the ray tracheids have not been figured, he goes so far as to question this unique example of their occurrence in the Cordaitean forms. I have carefully examined the type set of sections and have found no evidence to contradict Gothan's conclusion.

It should be noted at this point that there is no satisfactory evidence that Penhallow's "*Cordaites Clarkei*" is a Cordaites at all. The name was changed by Knowlton (18) solely on the basis of secondary wood characters, so that the occurrence of ray tracheids in *Dadoxylon Clarkei* need not be questioned merely because of their absence in other cordaitean forms.

As to the presence of ray tracheids in Callixylon, the evidence seems conclusive. In the first place there are two kinds of cells constituting the ray, thick-walled and thin-walled. The thick-walled elements have bordered pits in the upper, lower and side walls. Half-bordered pits are visible in the thin-walled elements. In *C. erianum* the thick-walled elements are lower than the thin-walled, showing that there are two distinct types of structures present in the ray. The bordered pits are sufficient evidence of their tracheal nature, in spite of the fact that they are absent in forms such as Cordaites, whose exact relation to Callixylon is unknown. A similar situation, according to Penhallow (22), is shown in the modern genus Abies, in which *A. balsamea* has rays made up entirely of parenchymatous elements, though all the other species have ray tracheids.

4. *Growth rings*

The question of the presence or absence of growth rings in Devonian woods has caused a great deal of comment and some conflicting statements, but the general consensus of opinion has been that they do not exist. Knowlton (17) says: "The Devonian floras indicate climatic uniformity by the absence of growth rings."

David White (32) states that there were inconspicuous annual rings in the Middle and Upper Devonian gymnosperms. Elkins and Wieland (11) and Hylander (14) mention vaguely defined growth rings in *Callixylon Oweni* and *C. Marshii,* respectively. Many of the species of Dadoxylon from the Carboniferous and Permian are described as having well-defined growth rings. Miss Goldring (12) describes them in the Carboniferous cordaite, *C. recentium.* Penhallow (22) says of *Cordaites Brandlingii:*

> I find that a very poorly defined growth ring is observable, but it is noted that such rings are not of the nature of those common to exogenous trees of higher temperate or sub-arctic regions, but are more comparable to those of sub-tropical regions where there is a constant tendency to continuous growth. Our figure shows that the limits of annual growth are indicated by a very

> unequal and narrow zone of tracheids which differs from those on either side by their shorter radial diameters.*** The zone itself is not more than a few tracheids wide, and the transition into elements of the surrounding structure takes place so gradually, both inwardly and outwardly, that it would be quite impossible to determine which is the inner or the outer face, were it not for the general disposition of the vascular elements.

The geological age of this specimen is not mentioned. Penhallow states for *Cordaites Newberryi,* probably from the Upper Devonian and Carboniferous, that in a radial extent of 17 millimeters there is no evidence of growth rings. He says that *Cordaites Clarkei* shows three vaguely defined zones in a radial distance of 15 millimeters, in which the tracheids appear to have a somewhat shortened radial diameter, but that the species agrees with the characters of the genus in the well-defined absence of growth rings. According to him, *Cordaites ouangondianum,* probably from the Upper Devonian and Carboniferous of New Brunswick, has no evidence of growth rings such as form a prominent feature in the original description (Dawson, 8). Similar statements are made about other forms.

From this it appears that, though Penhallow admitted the presence in most Devonian and Carboniferous forms of zones in which the tracheids are of a shorter radial diameter, he does not consider them as true growth rings.

The ultimate test of the nature of any such features as described above would be their origin. If the zones of radially shortened tracheids were actually caused by a slowing of growth due either directly or indirectly to climatic variation, growth rings would be represented, whether sharply defined or not. If the tracheids gradually shorten in radial extent, and then suddenly become longer, no matter if only to a slight extent, and this zone extended entirely around the stem, it would in all likelihood have been caused by corresponding conditions favorable to growth, hence a growth ring. This does not necessarily imply, however, that such rings are due to regular climatic fluctuations as summer and winter; they could just as well be due to extreme variations in the amount of rainfall, the only condition being that the plant be responsive to such changes.

Callixylon erianum, in which the secondary wood is 23 millimeters thick in the type specimen, has 5 complete concentric rings which extend completely around the stem (Pl. XVII, Fig. 1). Interspersed with these are several others which are less clearly defined. These closed rings show, passing from the inside toward the outside, a gradual shortening of the radial diameter of the tracheids up to a point where the outer limit of the season's growth is reached. Then there follows an abrupt change to tracheids of a much greater radial diameter commencing the next zone (Pl. X, Fig. 1). Measurements along the ring show that in a distance of 155 microns there are ordinarily from 1 to 2 or more tracheids at the outer boundary of the ring than on the inside of the adjacent ring. A few such measurements show results as follows:

"Summer wood," outside 155 microns	"Spring wood," inside 155 microns
6	4½
5½	4½
5½	4½
5	3½
5½	4½

In the Cheshire specimen of *C. Zalesskyi* there are no rings in a radial diameter of 4 millimeters. The Seneca Point specimen, in which the secondary wood is 9 millimeters thick, also shows no evidence of growth rings except a few very weakly defined areas of limited extent which cannot be traced for any distance around the stem.

In the same matrix with the last named specimen was a small fragment of wood (probably a root) which shows 10 rings in a radial extent of 6½ millimeters. These rings are faint, but at the same time definite. The "summer wood" zone consists of continuous rings of 1 or 2 tracheids in which the radial diameters are shortened as described by Penhallow. Measurements through and for some distance on each side of the "summer wood" show, however, that the shortening actually commences several cells back from the outer boundary of the ring, and the first circle of tracheids of the adjacent "spring wood" has a greater diameter than the circle of cells just inside the shortest "summer wood" tracheids (Pl. XVIII, Fig. 1). This shows, then, that growth gradually came to an apparent standstill and later was rather suddenly resumed. The measurements also show that the second circle of "spring wood" tracheids has a greater thickness than the first one, which indicates that growth was not as rapid at first as it was later on. Here, however, the change is much more abrupt than on the other side.

Measurements of the tracheids indicate, therefore, actual growth rings in these woods. Whether they are annual rings in the accepted sense is doubtful, but they were doubtless due to changes of some sort in the environment which made conditions more favorable for growth at times.

Some modern temperate zone angiosperms, *Juglans cinerea* Linn. for example, have rings which are but little more clearly defined than in the specimen last described (Pl. XIV, Fig. 2).

A situation somewhat similar to that in *C. erianum* was found by Coster (6) in *Pinus Merkusii* from Sumatra. The rings in this form consist of a zone of cells in which the radial diameters are slightly shortened and the zone merges gradually into the larger celled tissue on either side. These rings are not always complete. In the older trees they were sharp and of the ordinary coniferous type, but intermixed with them were the sporadically arranged indistinct rings. *Podocarpus cupressus* (Coster, 6), from East Java, contained a few complete rings unequally spaced, and between them were indistinct zones which extended only part way around the stem. The similarities between these rings and those in the Devonian woods suggest that they may represent a similar environment. The deciduous trees of East Java are without leaves for one to three months during the dry season.

Thomson (30) describes such rings in Araucaria. They represent all stages from a clear demarcation of the season's growth to those in which there is no determinable boundary.

5. *Convoluted tracheids*

A very striking feature seen in the tangential sections of some specimens is the presence of areas of convoluted tracheids. In these areas the tracheids depart from their usual elongated form and assume various fantastic shapes (Pl. VIII, Fig. 4), creating a situation almost impossible to describe accurately. These areas are generally round or oval and of about the same diameter as the cross-section of an outgoing trace. In approaching one of these areas from either above or below the tracheids separate; some of them bend inward and mingle with the convoluted mass; the others bend on around the mass and converge again on the opposite side. The tracheids within the area have the appearance of being arranged around a center, or usually there seem to be several centers around which they tend to converge, giving the aspect of a number of whirlpools confined to a small area. They are the most conspicuous in the specimen of *C. Zalesskyi* from Seneca Point.

Similar structures have been mentioned and briefly described in other forms. Scott and Jeffrey (27) figure such structures in *Archeopitys Eastmanii*, which they suggest may be broadened rays of some sort. Sahni and Singh (23) figure similar structures in *Dadoxylon Arberi* and consider them to be traces.

Of these two suggestions the trace theory is the most plausible, but from their appearance in the material under consideration they seem to be associated with the traces rather than constituting traces themselves. A radial section shows quite a disturbance in the secondary wood where it closes over and buries the end of a trace where a leaf has fallen (Pl. IX, Fig. 1). A mass of parenchyma is formed immediately over the end and farther out. As nearly as the material at hand permits one to judge, the closing xylem is much distorted for some distance, or this distortion may even persist as a radial strand throughout the width of the secondary wood.

Root Structure

Several roots belonging to Callixylon were found during the course of this study. Transverse sections of these specimens show a group of rather large round tracheids in the center of the stele with the protoxylem points at the edge and in contact with the secondary wood. The structure is, therefore, similar to that in the roots of the present-day gymnosperms and higher plants (Pl. XIX, Fig. 1).

Roots were found in four localities: Cheshire ravine, Seneca Point ravine, west shore of Canandaigua Lake north of Seneca Point and the Cornell campus.

During the process of calcification the growing crystals produced a splitting and a forcing apart of the tissues near the center of the root, with the consequent destruction of many of the finer details. The number of primary xylem arcs is, therefore, indeterminable, but there appear to be from 3 to 5, the number possibly not being constant. The Cheshire specimen which is best preserved appears to have 4.

None of the roots were found attached to the stems, but in all specimens the two were found in close association. They were all small, varying in diameter from 5 to 15 millimeters.

The secondary wood is much like that of the stem although there are some minor differences. The tracheids are generally thinner-walled and more variable in shape and size. Faintly developed growth rings are abundant.

The bordered pits on the radial walls of the tracheids are grouped after the Callixylon fashion. The size of the groups is variable, ranging from 7 to 40 pits each and sometimes more, but these larger ones are probably multiple groups. The number of pits per group is directly related to the number of rows of pits per tracheid, but they seem to be more independent of the size of the tracheid. The following table shows the relationship:

Specimen No.	Diameter of tracheid in microns	Rows of pits per tracheid	No. of pits per tracheid	Average
400	34 × 46	2–3–4–5	15–40	24
401	31 × 33	1–*2*–3 *	7–24	14
501	33 × 41	1–*2*–*3*–*4* *	9–21	14–15
507	32 × 36	2–*3*–4 *	11–36	21
508	33 × 42	2–3–*4*–5 *	14–28	21

* Figures in italics show the predominating condition.

The large pit groups may, therefore, be primitive because in the form with them present there also seems to be more of a gradation into continuous pitting typical of Dadoxylon. Moreover, this feature is to be expected inasmuch as roots in general tend to retain primitive characters.

The Phloem

A small amount of the inner portion of the phloem was found attached to the specimen of *Callixylon Zalesskyi* from Bristol Center. The amount preserved is small, being less than one millimeter thick, but it is of especial interest because it is the first instance of phloem being observed in connection with the genus. Although it is small in amount and remains in only a single small fragment, a little of its general structure can be made out.

It consists of alternating layers of empty cells and cells with dark contents. The former are elongated radially and intermixed with them are shorter cells, some of which contain a dark substance resembling resin. This tissue is only a few cells thick. The layer with dark contents is 2 or 3 cells in extent and consists of cells of about the same size and shape as the tracheids (Pl. XIX, Fig. 2). No idea of the thickness of the phloem can be derived from this specimen.

This phloem seems to differ from the phloem of *Cordaites hamiltonense* as described by Penhallow (22). It is differentiated into 3 zones, the inner, the middle and the outer. This inner zone, which probably compares to that described above consists of isodiametric, thin-walled parenchyma elements. Scattered throughout this region, but chiefly forming a limiting layer on the outer surface, are numerous resin-bearing elements. Sclerenchyma cells are intermixed with the parenchyma.

CONCLUSION

Probable habit of the plant

An attempt to describe a Callixylon plant would be premature, but there are some facts which permit one to venture a few suggestions as to its probable habit.

The largest form studied, *Callixylon erianum,* had a stem about two inches in diameter. The material of most of the other forms was smaller, one inch or less. Clarke's specimen of *C. Zalesskyi* from Bristol Center was a slab taken from a two-foot length of a straight stem which must have been 2 or 3 inches in diameter. This specimen contained a branch which departed at an angle of 45 degrees, the only example of branching observed.

Some of the carbonized impressions which are associated with Callixylon at Bristol Center are as much as an inch wide, three feet long, straight, and show no sign of branching. Similar carbon strips have been observed in Taughannock Gorge (see Pl. II, Fig. 2), Lodi Glen, and at other places where the Portage formation is exposed. The pith cast of these strips is smooth, a character indicative of Callixylon.

The size and length of some of the preserved specimens, together with the well-developed gymnospermous wood, suggest a tree-like habit in which the branches were few but long and straight. This straightness is the chief objection to the idea, suggested by a slight but natural flattening of some of the specimens, that the plant was possibly a vine.

In *C. Zalesskyi,* four traces were found to arise in a length of about two centimeters, and nine could be seen in various stages of departure. Since no two of them were vertically aligned, the leaves were spirally arranged and the phyllotaxy was probably high.

The size of the traces and their distribution would suggest that the leaves were larger than those of modern conifers, but on the other hand they were probably smaller than the very large leaves of such forms as *Cordaites laevis* or *C. angustifolia.* The fact that the trace shows no sign of division at the outer boundary of the secondary wood suggests that it remains single throughout. It is plausible, therefore, to consider the leaves of this plant as rather simple, probably 3 or 4 inches long, an inch wide, and supported on a short petiole. Grand' Eury's restoration of Dorycordaites (Coulter and Chamberlain, 7, p. 164), but with somewhat smaller and more numerous leaves, is suggestive of this plant.

Abundance and distribution of Callixylon in the past

The occurrence of Callixylon in two continents, Europe and North America, indicates a wide distribution for the plant. This, together with its high specialization, probable arboreal habit, and abundance of remains in certain strata suggests that it was one of the common plant types of the Upper Devonian period. The predominance of only a single plant type in a formation is a condition not unusual, but in this case its occurrence over such a wide area without the association of other forms is difficult to explain except on the basis of its being the only plant of the time with resistant tissues. Also the absence of very large trunks is unexplainable unless we assume that the remains are only driftwood and the large trunks were unable to drift away in the shallow water to localities in which deposition was taking place. Under such circumstances it is conceivable that only the smaller branches would be preserved.

Relationship to other forms

The affinities of Callixylon are briefly discussed by Scott (25, p. 263) and by Zalessky (35) in his original description of the genus. The latter author compares it to *Pitys antiqua* on the basis of pith characters and to Calamopitys (Eristophyton) and *Parapitys Spenceri* on similarities in the secondary wood. He points out that it differs from *Pitys antiqua* in having narrow rays. Scott says that it differs from Pitys by the primary xylem strands being in actual contact with the secondary wood instead of being some distance out in the pith. He does not consider it close to *Parapitys Spenceri*, in which the primary wood is endarch.

The present study has brought out a few additional points for comparison. The leaf-gap condition in Callixylon is similar to that in *Calamopitys americana* and *Archeopitys Eastmanii* of lower Carboniferous age. In both these forms the reparatory strand is continuous and not broken at the point of departure of the trace. The pith of Callixylon, with a few medullary tracheids, bears some resemblance to *Calamopitys americana*, in which such tracheids are more numerous. A resemblance to *Calamopitys fascicularis*, in addition to those pointed out by Zalessky, is the fact that the primary wood bundles enlarge slightly and become centrally mesarch previously to dividing to send off a trace. Lower down the protoxylem approaches the inner edge of the bundle, leaving only 2 to 4 cells of centripetal metaxylem. Another resemblance between the two forms is the number of primary wood bundles, which is 8 or 9 in *C. fascicularis* and 8 to 20 in Callixylon. No medullary tracheids are reported in *C. fascicularis*.

As to the relation with Pitys and Archeopitys, a few additional facts can be given. Medullary bundles occur in both these genera, but the situation is quite different from the few and scattered medullary tracheids of Callixylon. There is also quite a difference in the number of primary wood bundles; there are 30 or 40 in *Pitys antiqua*. These differences would seem to suggest affinities more in the direction of the Calamopityeae and hence toward the Pteridospermae rather than toward the Cordaitales.

Concerning the little known *Paleopitys Milleri* M'Nab (Kidston and Lang, 16), there is but slight suggestion of any affinity with Callixylon. The equal distribution of the pits over all four walls of the tracheids can hardly be regarded as comparable to the tangential pitting of Callixylon because in the latter case they are irregularly distributed and present a marked contrast to the regular groups in the radial walls. Although its affinities are undetermined, the tracheids of the secondary wood are said to be pteridospermous. This form is of some interest, nevertheless, because of its great age (Middle Devonian). For this reason the possibility of its being ancestral to Callixylon is greater than for contemporary or later forms, as Pitys or Calamopitys.

The abundance of Callixylon remains furnishes evidence of its being one of the dominant plant types of the Upper Devonian period. While it may more closely resemble the Calamopityeae, and the Pityeae than the Cordaiteae, it is of interest to compare it with the latter family on account of Cordaites being the dominant higher gymnosperm of the Carboniferous period. The comparative abundance of Callixylon and the rarity of the Calamopityeae and the Pityeae place Callixylon in a very important position phylogenetically.

This importance which we assign to Callixylon is due to its high degree of specialization and its age. While it retains one primitive character, the mesarch primary wood, the plant itself cannot be considered as primitive, but rather it shows evidence of being the termination of a long — or if short, intensive — evolutionary line.

Evidence in support of this is the relatively brief transition zone of 7 or 8 cells from scalariform to pitted tracheids, much less even than other Cordaitean and Dadoxylon forms of later periods. This brief transition zone is generally considered to be an advanced character. The evidence of advancement furnished by the ray tracheids is also positive. Ray tracheids are considered by Jeffrey (15) to be primitive and by Penhallow to be derived. In Callixylon we find species in which they occur in abundance, as *C. erianum, C. Zalesskyi* and *C. bristolense,* and also forms in which they are rare. Also *C. Newberryi* (Penhallow, 22) and *C. Oweni* (Elkins and Wieland, 11) are described as having rays with thin-walled cells. So if either of these characters is derived, it is represented in Callixylon. In *C. erianum* the ray tracheids not only are abundant, but are distributed in a very orderly and characteristic fashion.

The absence of ray tracheids in Cordaites, which because of its endarch primary wood is considered to be higher in the evolutionary scale than Callixylon, cannot be viewed as evidence of Cordaites being primitive. A point in this connection is the grouped pitting of Callixylon which is certainly a very specialized character, as against the continuous pitting of Cordaites, and yet the secondary wood of Cordaites is hardly to be looked upon as primitive when compared even with modern gymnosperms. The important point is that Callixylon developed this one very distinctive character which Cordaites did not do. It is equally possible, then, that ray tracheids are a derived character and represent the same sort of independent development.

The absence of a leaf gap in this genus suggests all kinds of possibilities for its pteropsid or lycopsid affinities. Judging from this character alone, one would be inclined to refer to it as a member of the Lycopsida. On the other hand, because of its apparent affinities with the Pteridospermeae and the Cordaitales, it could be placed with confidence in the pteropsid group. This would imply the presence of leaf gaps, but a series of transverse and longitudinal sections through the region of a departing trace shows that no such gap is present.

On the basis of this fact it appears that Callixylon, along with *Calamopitys americana* and *Archeopitys Eastmanii*, which show a similar leaf trace condition, represents the termination of a very ancient group of plants from which the Pteropsida developed at a very early period. Callixylon, being the oldest known member of this line, which may conveniently be referred to as the Archeopteridopsida, was also the most highly specialized of this probably much diversified group.

The occurrence of scattered medullary tracheids in Callixylon would then suggest its origin from a previous protostelic complex of which the Middle Devonian *Paleopitys Milleri* might have been a representative. The mixed pith of *Calamopitys americana* indicates affinity with a protostelic group, but this species had not reached the high degree of specialization in the lower Carboniferous which had been attained by Callixylon during the Upper Devonian.

All the evidence at hand points, therefore, to Callixylon as a highly organized plant which probably flourished during the Upper Devonian to practically the same extent that Cordaites did during the Carboniferous. It probably was not in the line of direct descent of later forms, but reached its climax and disappeared at the end of the Devonian or early Mississippian. Its affinities, therefore, must be looked for farther back where it probably sprang from a stock common to both the Pteridospermeae and the Cordaitales.

Callixylon and plant evolution

The Devonian has always been regarded as the period during which the seed plants originated. Scott (26) mentions four great plant transformations: the Silurian; the Middle Devonian, the period during which the relatively simple Psilophytales were replaced by the higher Paleozoic forms; the late Permian, in which the plants of the coal measures were replaced by the cycadeoids; and the Cretaceous, the period during which our modern flowering plants appeared and became dominant. The logical conclusion from this would be that land plants originated during the Silurian or possibly during the Ordovician.

Scott's viewpoint is criticized by Berry (3) when he cites a number of highly developed forms occurring in the Devonian. His outstanding examples are *Protolepidodendron primaevum,* the "Naples tree," *Paleopitys Milleri* from the Middle Devonian of Scotland, and the four known species of Callixylon. He also mentions the somewhat problematic *Archeoxylon Krasseri*[1] from the pre-Cambrian of Bohemia. Speaking of *Paleopitys Milleri* and Callixylon he says:

> It is true such types have not been discovered in the lower Devonian or earlier horizons, but such an advanced anatomical type did not evolve or become widely distributed in a short time, and they will eventually be discovered.

Therefore Berry would maintain that the transformation was gradual and commenced much farther back than the Middle Devonian.

Berry's contention is open to criticism in two points. The first one is that he considers these plants to be older than they really are. The "Naples tree" which he refers to the Middle Devonian actually came from the Hatch shale of the Upper Devonian. The same error is made with *Callixylon Oweni,* which came from the Genesee shale horizon. The exact horizon from which *C. Newberryi* and *C. Marshii* came is uncertain, although the original descriptions specify the middle.

The second criticism is that comparatively sudden plant transformations have been known to occur. The sudden appearance of an abundant angiosperm flora during the Cretaceous shows that evolution proceeds rapidly at times and it is equally possible that a similar transformation occurred during the Devonian.

Whichever of these two opposing views is taken, the present study serves to emphasize Scott's statement (25, p. 264) that Callixylon has the most highly differentiated wood structure and is also the oldest member of the Pityeae. The considerable amount of variation shown by the different forms (here considered as species) suggests a diversified genus terminating a pronounced evolutionary process which was either gradual and long or intense over a shorter period.

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[1] In a recent conversation Dr. Kräusel expressed doubts whether Archeoxylon was pre-Cambrian.

The chief interest in Callixylon lies, therefore, in the fact that it is a highly specialized plant which occurred as far back as our knowledge of seed plants extends. Whether it was pteridospermous or cordaitean or something different, is a question to be settled only on the acquisition of more information.

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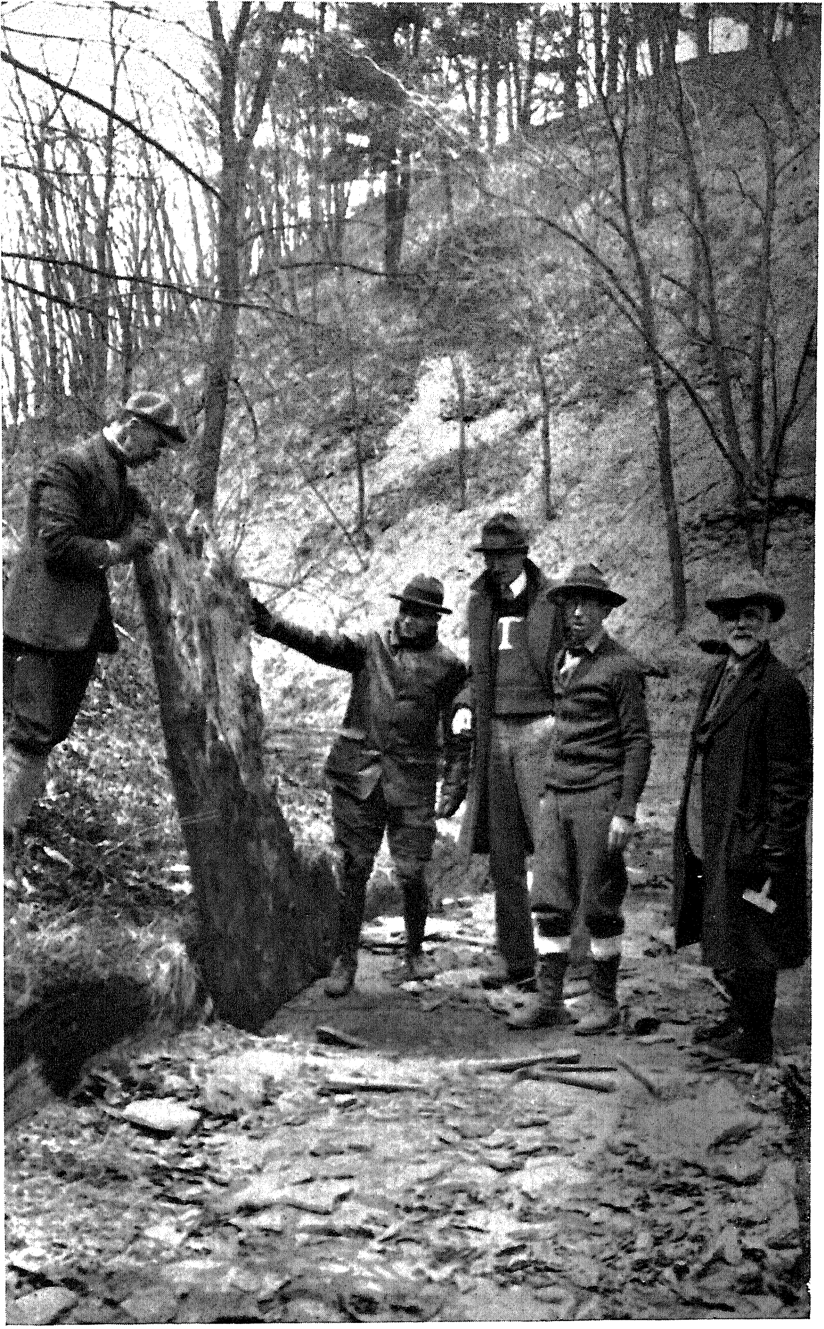


Slab of Genundewa limestone in creek at Bristol Center
Left to right: L. W. Sharp, F. A. Hodges, A. E. Alexander, L. C. Petry, G. R. Wieland

PLATE II

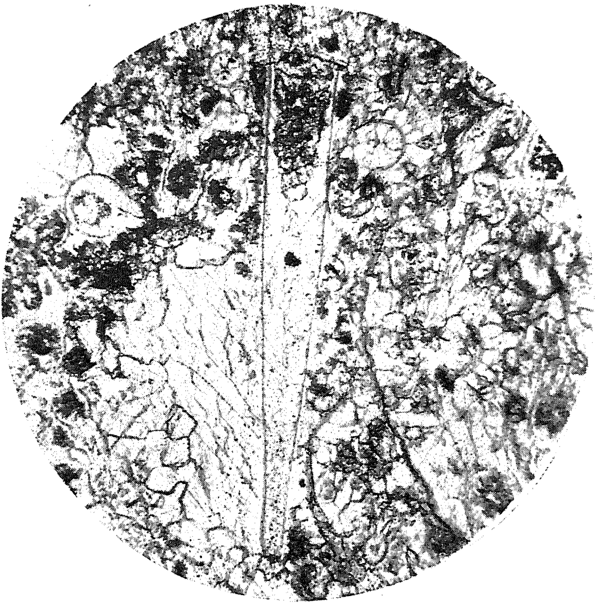
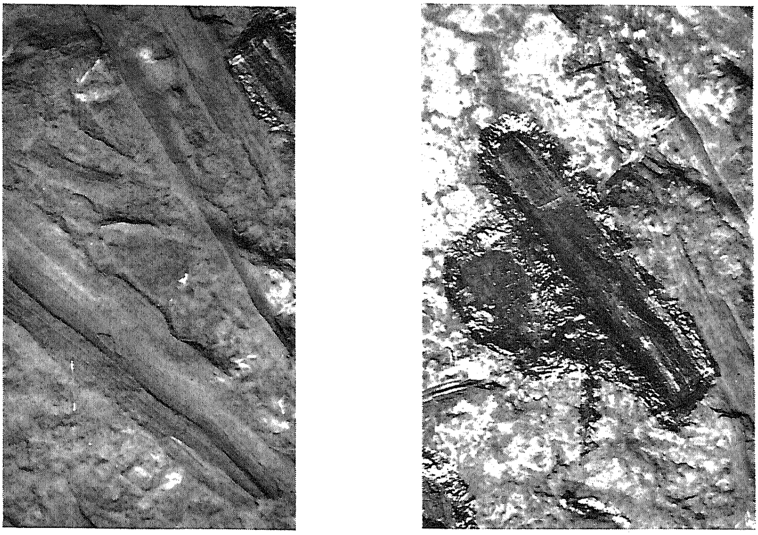


FIG. 1. Longitudinal section and cross-sections of shells of *Styliolina fissurella* in Genundewa limestone. × about 55



FIGS. 2 a and b. Flattened and bituminized woody stems on sandstone slab. From Taughannock Falls State Park. The figure at the right was shellacked to hold the material together. × about $\frac{1}{4}$

PLATE III

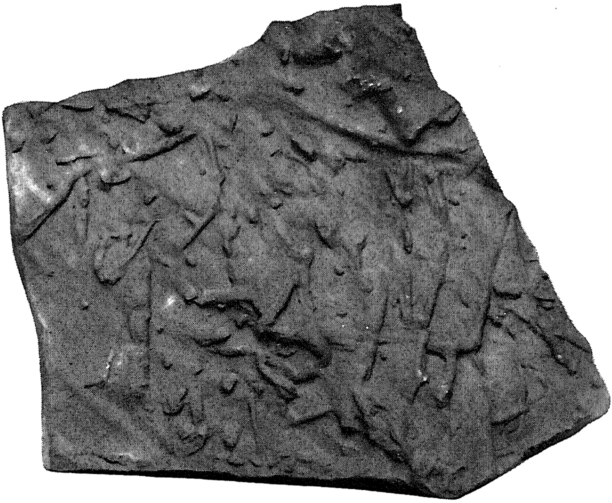


FIG. 1. "*Fucoides graphica*" Vaneuxem from Portage sandstone. South Hill, Ithaca. × $\frac{1}{3}$

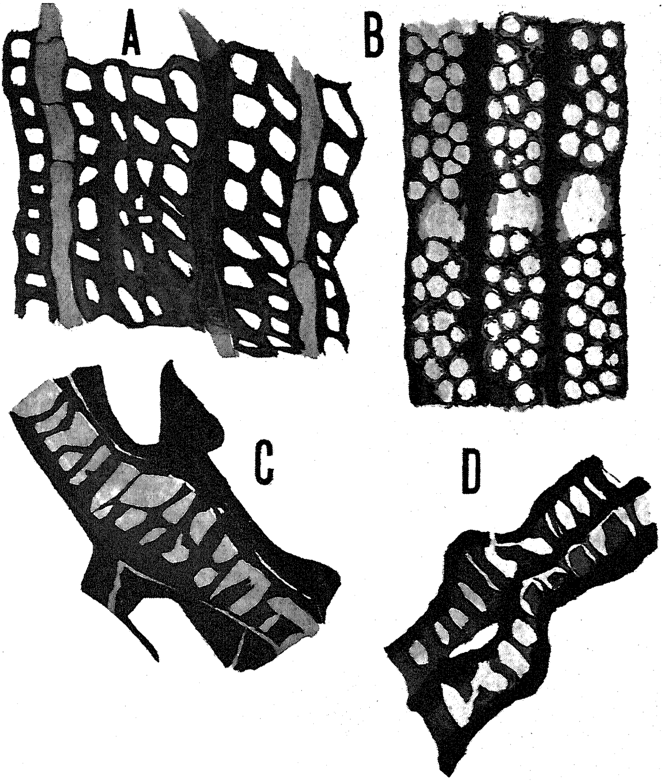


FIG. 2. *Callixylon Marshii* Hylander. *a*, transverse; *b*, radial; *c*, transverse showing portion of ray, greatly enlarged; *d*, portion of biseriate ray. Figures prepared by Miss C. A. Black

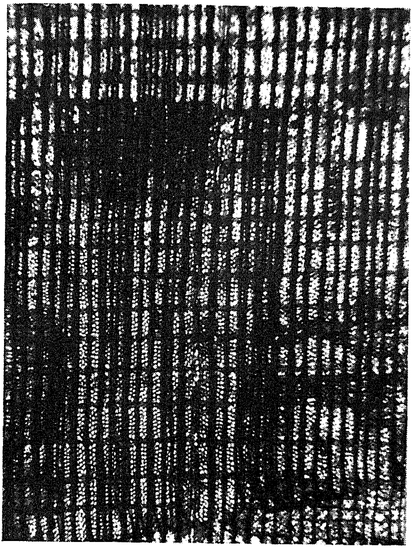


FIG. 1. *Callixylon Zalesskyi* Arnold, sp. nov. Radial section showing radially aligned pit groups. × about 75

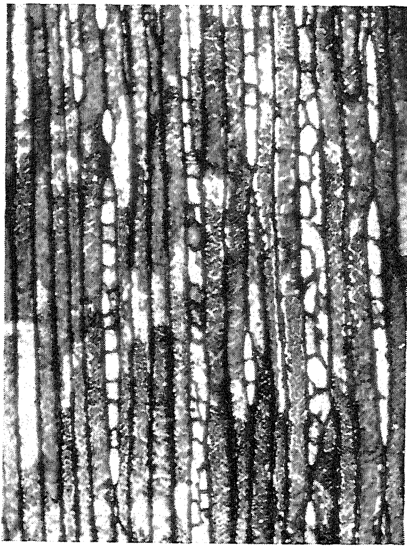


FIG. 2. *Callixylon Zalesskyi* Arnold, sp. nov. Tangential section showing uniseriation and biseriation of the rays. × about 80

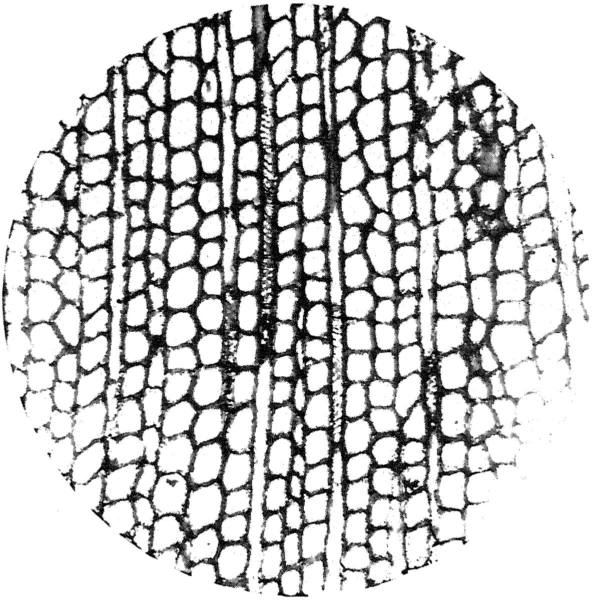


FIG. 3. *Callixylon Zalesskyi* Arnold, sp. nov. Transverse section showing gymnospermous character of the secondary wood and pitting on the horizontal walls of the ray tracheids. × about 85

PLATE V

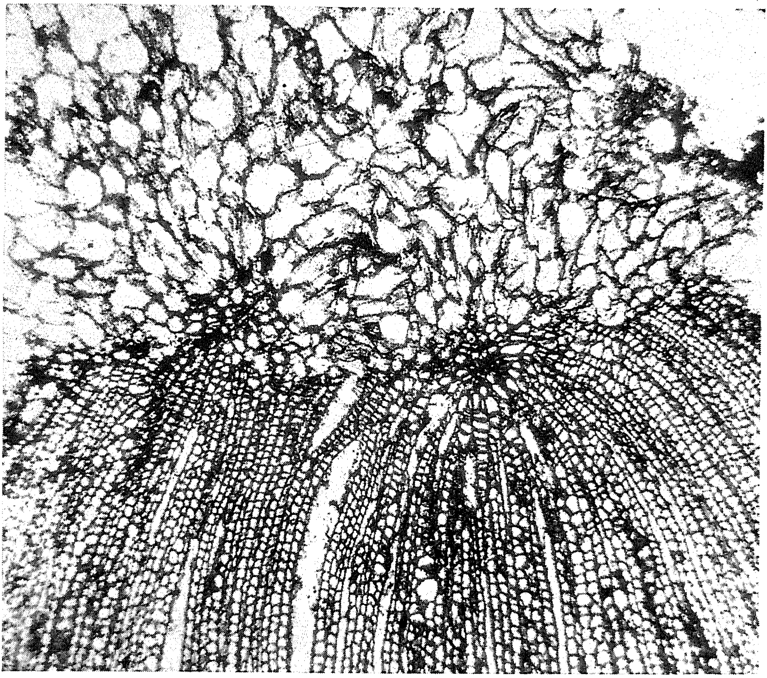


Fig. 1. *Callixylon Zalesskyi* Arnold, sp. nov. Mesarch primary wood bundles. × about 30

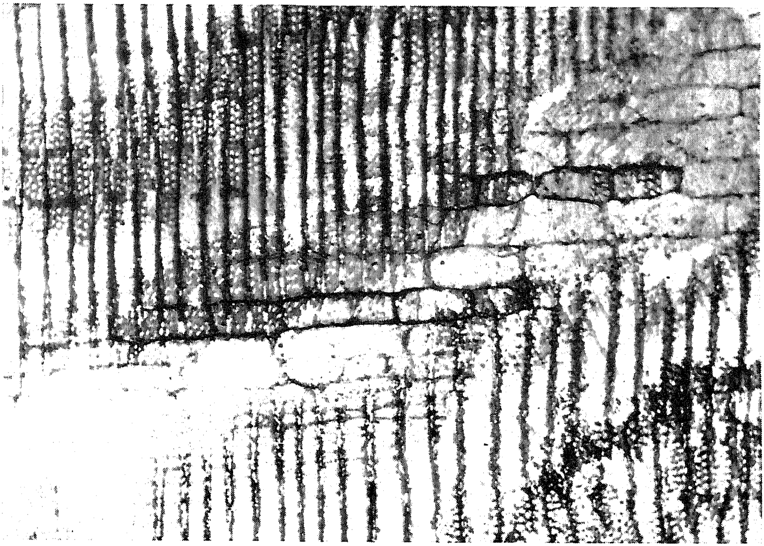


Fig. 2. *Callixylon Zalesskyi* Arnold, sp. nov. Radial section showing size, shape and arrangement of the ray tracheids. × about 80

PLATE VI

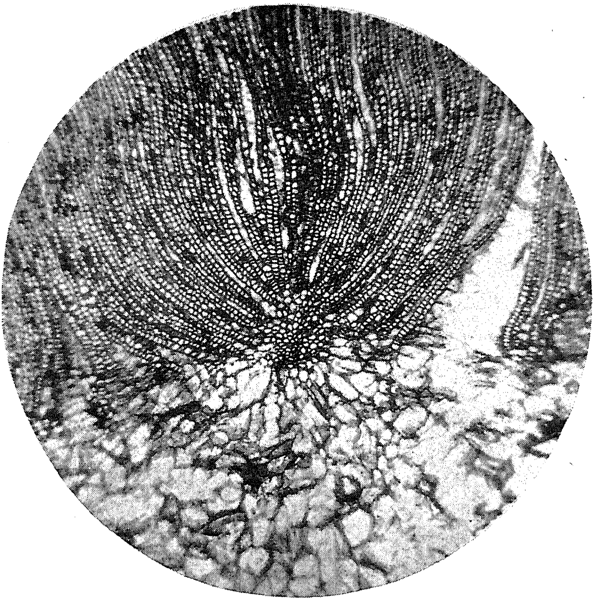


FIG. 1. *Callixylon Zalesskyi* Arnold, sp. nov. Primary wood bundle commencing to enlarge prior to its division to form a trace. × about 30

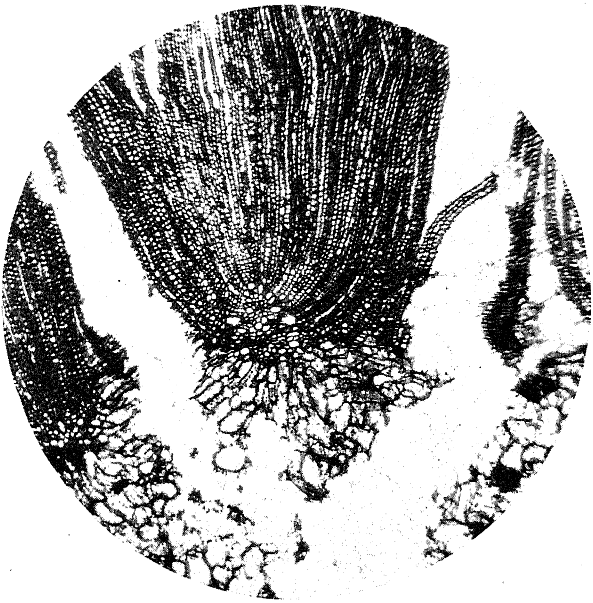


FIG. 2. As in Figure 1, but at a higher level and showing the divided bundle. × about 30

PLATE VII

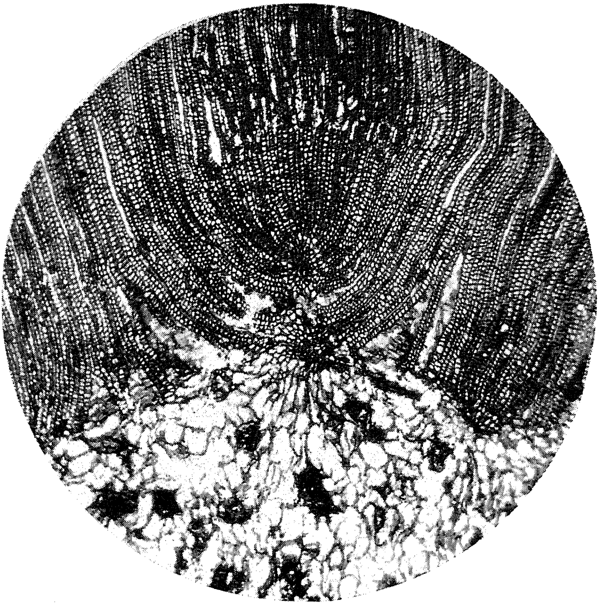


FIG. 1. *Callixylon Zalesskyi* Arnold, sp. nov. Continuation of Plate VI. The two bundles have completely separated. × about 30

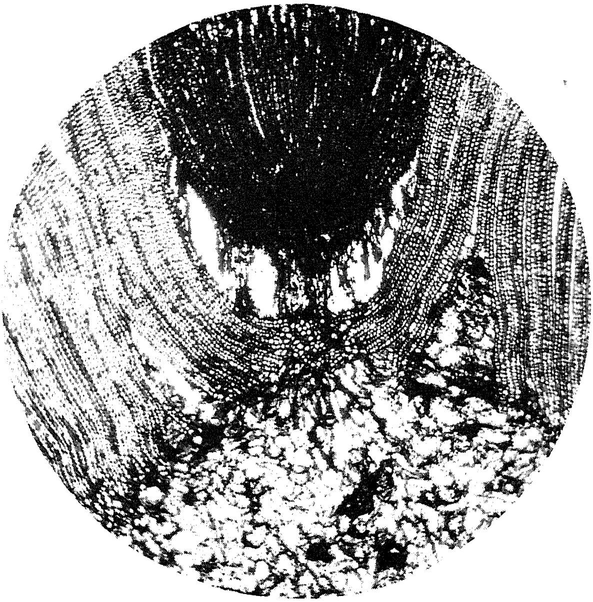


FIG. 2. Continuation of Figure 1. The trace bends sharply outward leaving a parenchyma-filled area between it and the reparatory strand. × about 30

PLATE VIII

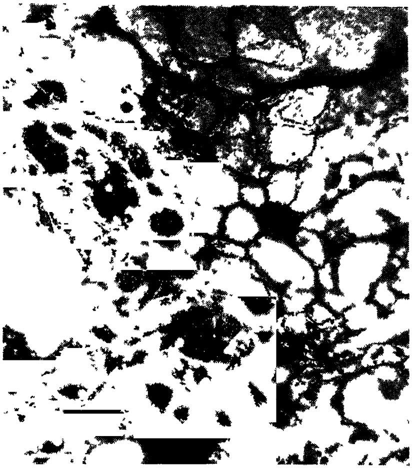


FIG. 1. *Callixylon Zalesskyi* Arnold, sp. nov. Transverse section through pith showing a group of pith tracheids. × about 90

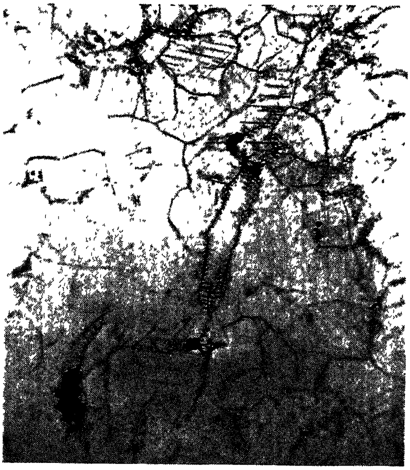


FIG. 2. *Callixylon sp.* (No. 11081). Isolated pith tracheids in longitudinal section. × about 90

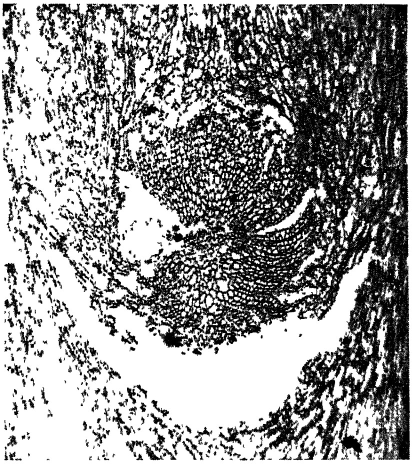


FIG. 3. *Callixylon Zalesskyi* Arnold, sp. nov. Cross-section of outgoing trace with secondary growth. × about 35

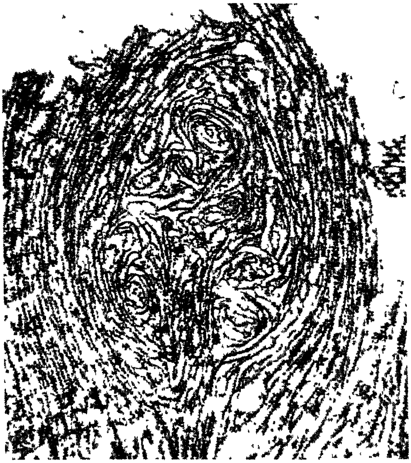


FIG. 4. *Callixylon Zalesskyi* Arnold, sp. nov. Convoluted tracheids. × about 25

PLATE IX

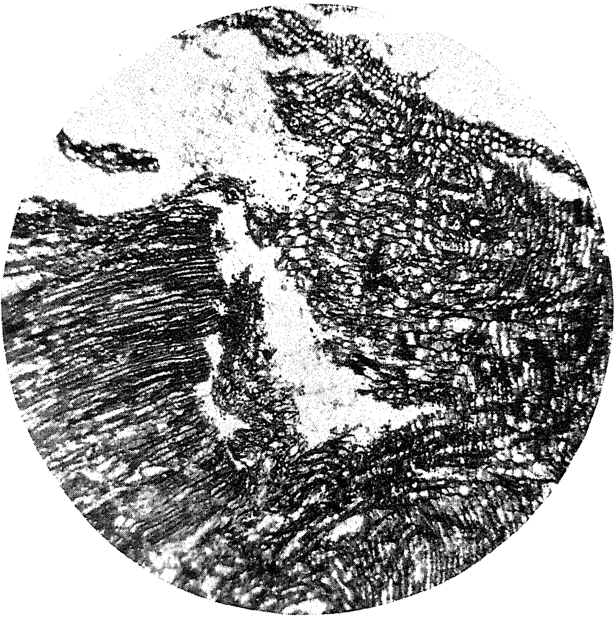


FIG. 1. *Callixylon Zalesskyi* Arnold, sp. nov. Radial section showing end of trace buried by subsequent secondary growth. × about 35

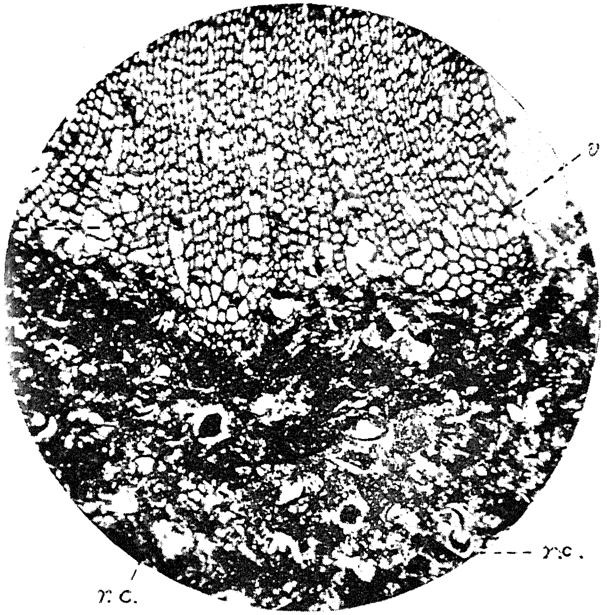


FIG. 2. *Dadoxylon Clarkei* Dawson. Transverse section through primary wood region. After Penhallow. × about 45

PLATE X

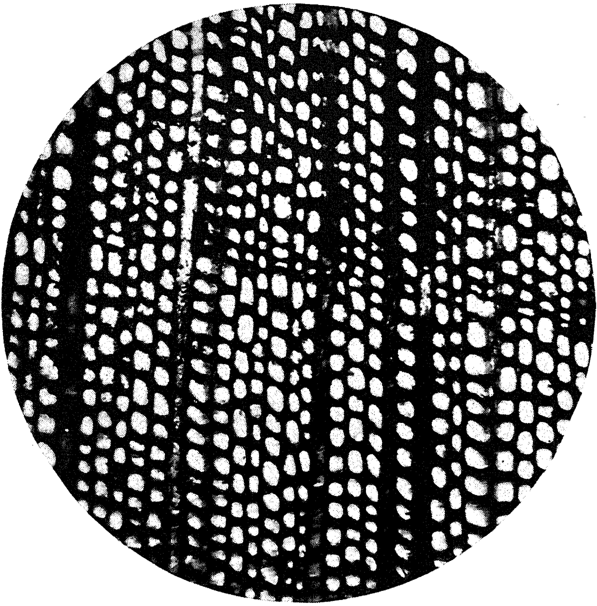


FIG. 1. *Callixylon erianum* Arnold, sp. nov. Transverse section showing thin zone of "summer" wood. × about 55

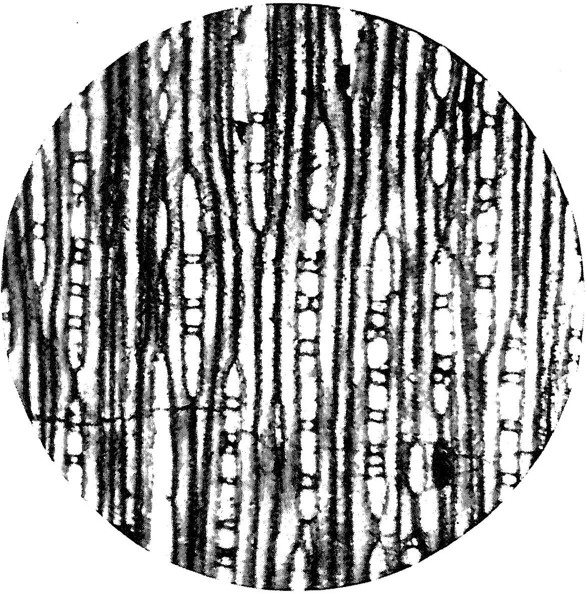


FIG. 2. *Callixylon erianum* Arnold, sp. nov. Tangential section showing relative size, shape and distribution of ray tracheids and ray cells. Partial biseriation is also visible. × about 65

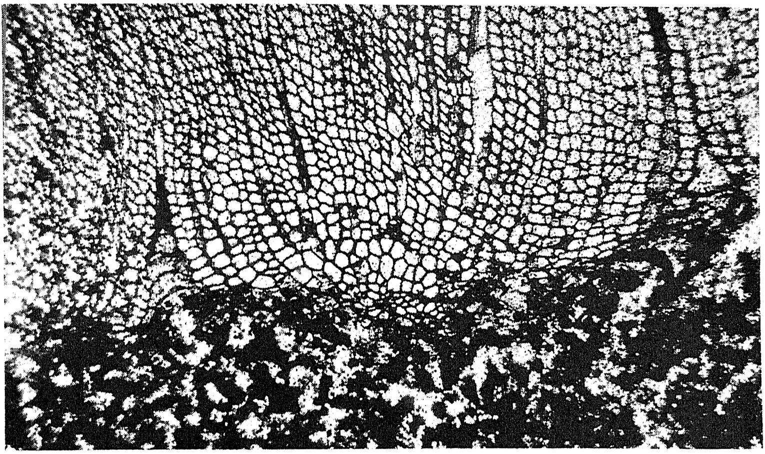


FIG. 1. *Callixylon erianum* Arnold, sp. nov. Transverse section showing mesarch primary wood bundles and broadening of the rays as they approach the pith. × about 35

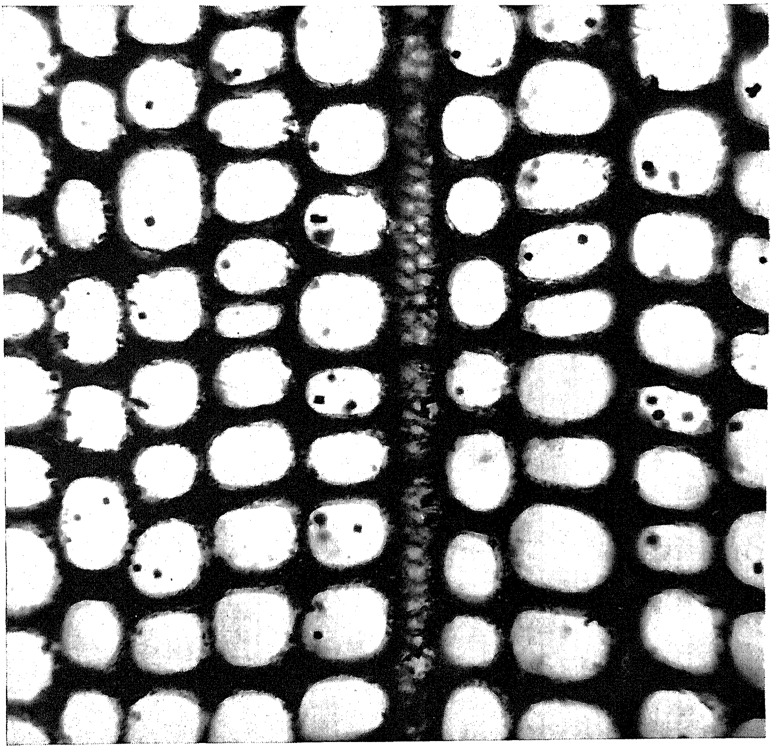


FIG. 2. *Callixylon erianum* Arnold, sp. nov. Enlarged portion of secondary wood showing thick-walled, regularly arranged tracheids, and the pitting on the horizontal walls of the ray tracheids. × about 300

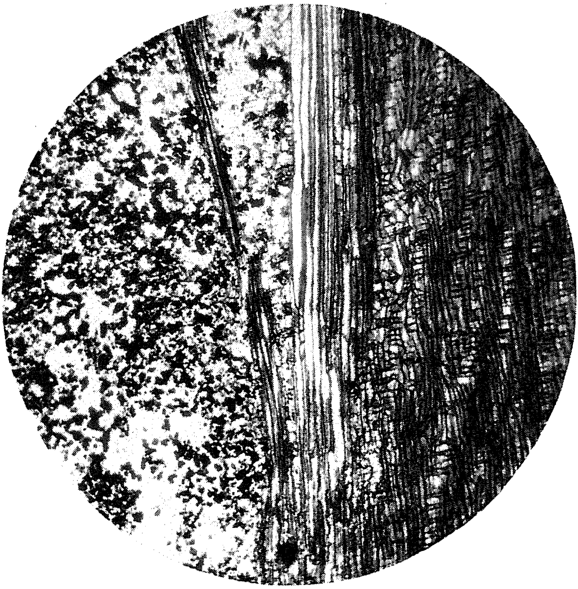


FIG. 1. *Callixylon erianum* Arnold, sp. nov. Longitudinal section through primary wood bundle showing the origin of the trace. The reparatory strand continues uninterrupted from the point of division of the bundle and in the figure it swings slightly to the left. × about 25

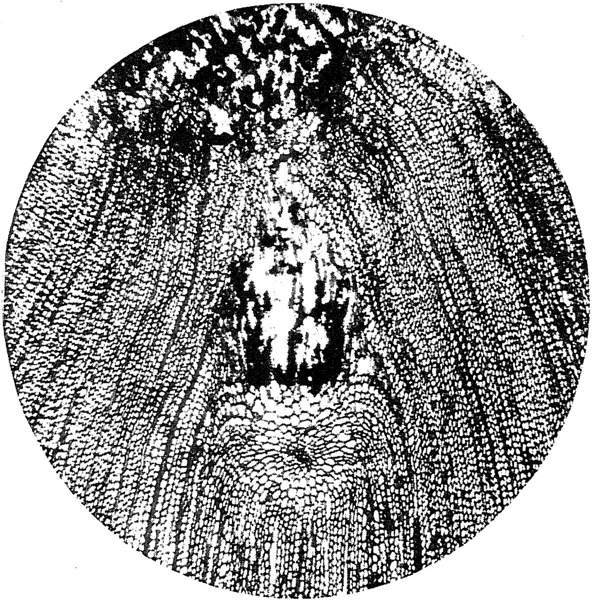


FIG. 2. *Callixylon erianum* Arnold, sp. nov. Transverse section just above point of origin of the trace. × about 25

PLATE XIII

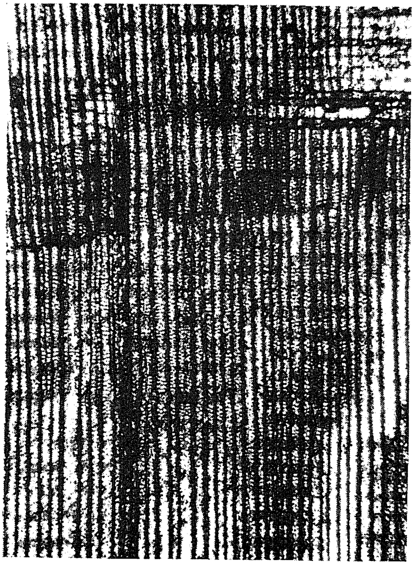


FIG. 1. *Callixylon erianum* Arnold, sp. nov. Radial section through secondary wood. × about 40

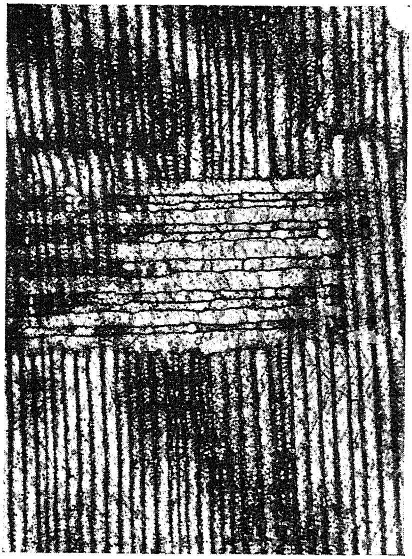


FIG. 2. *Callixylon erianum* Arnold, sp. nov. Radial section showing relative, shape and arrangement of ray tracheids and ray cells. × about 35

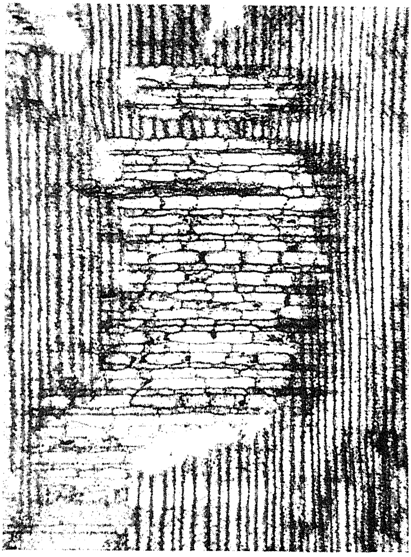


FIG. 3. *Callixylon erianum* Arnold, sp. nov. As in Figure 2, except that it gives a more adequate idea of the height of the ray. × about 35

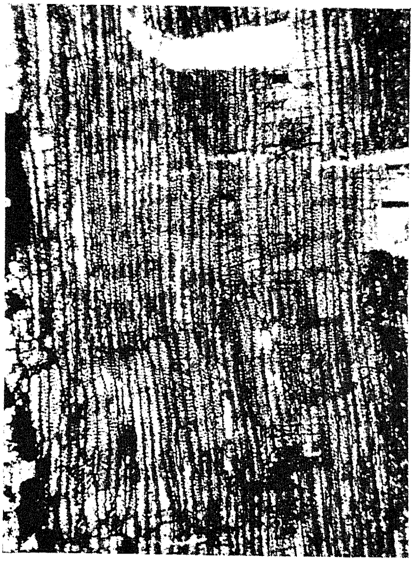


FIG. 4. *Callixylon sp.* (No. 11080). Radial section showing irregularity in pit grouping. × about 45

PLATE XIV

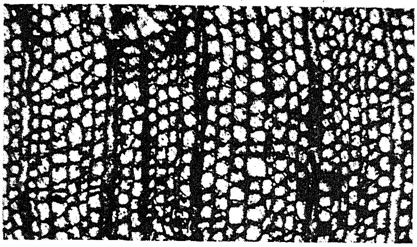


Fig. 1. *Callixylon bristolense* Arnold, sp. nov. Transverse section. × about 80

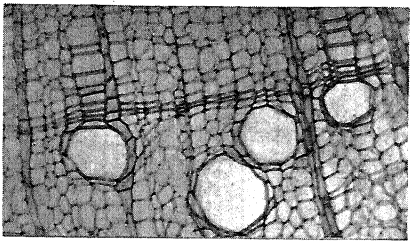


Fig. 2. *Juglans cinerea* L. Narrow summer wood zone in many respects similar to that found in *Callixylon erianum* and *C. Zalesskyi*. × about 140

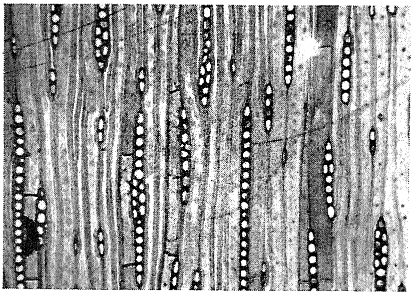


Fig. 3. *Sequoia sp.* Tangential section showing partially biseriate rays which in many respects resemble those of *Callixylon Oweni* and *C. mentethense*. × about 70

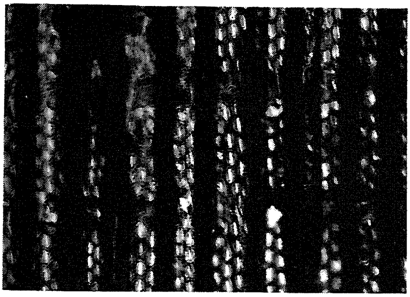


Fig. 4. *Callixylon bristolense* Arnold, sp. nov. Radial section showing vertical pit orifice. × about 30

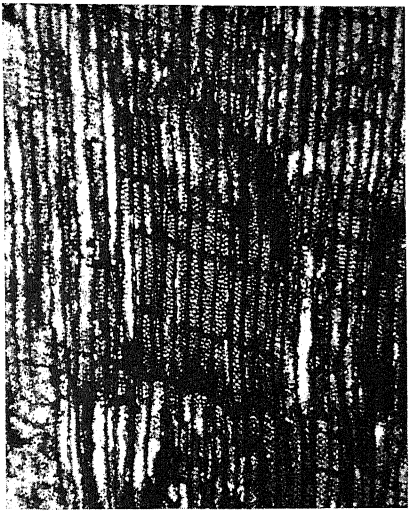


Fig. 5. *Callixylon sp.* (No. 11082). Radial section showing very large pit groups. × about 60

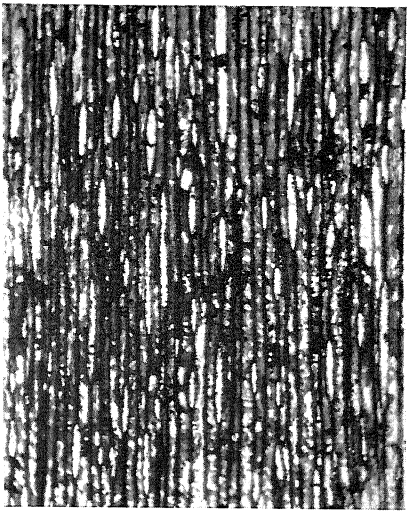


Fig. 6. *Callixylon sp.* (No. 11083). Tangential section showing very small and numerous rays. × about 80

PLATE XV

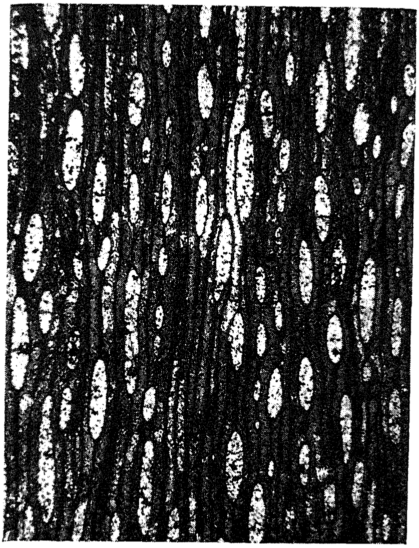


FIG. 1. *Callixylon mentethense* Arnold, sp. nov. Tangential section showing broad, oval rays. × about 35

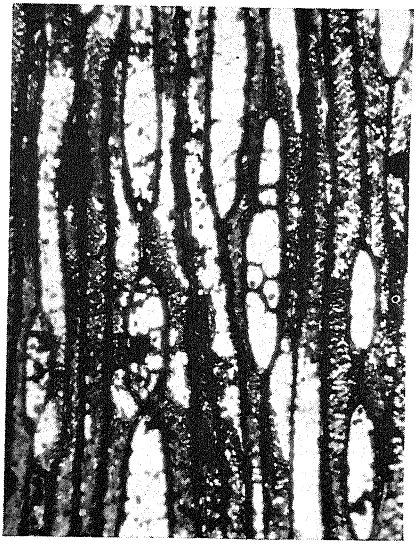


FIG. 2. *Callixylon mentethense* Arnold, sp. nov. Biseriation in rays. × about 90

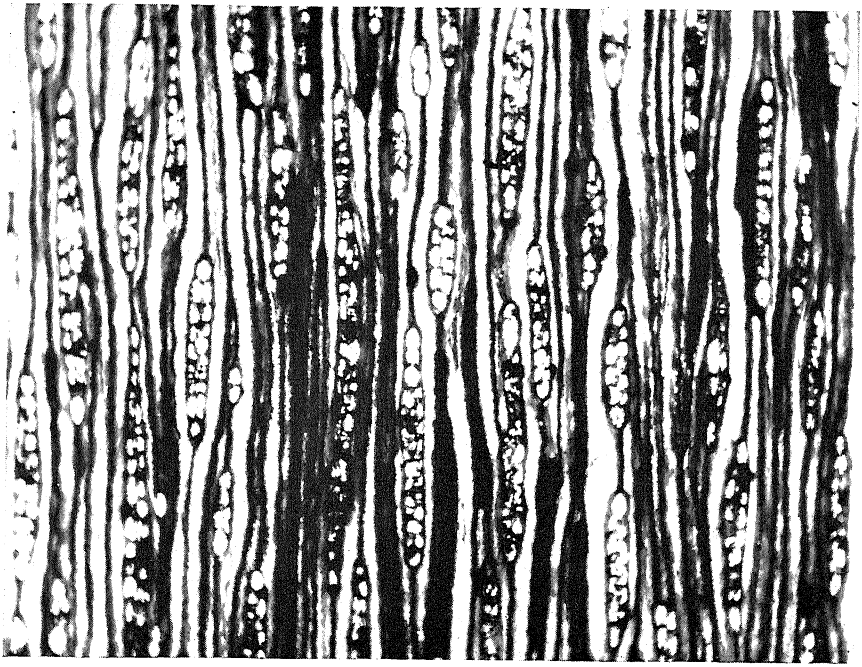
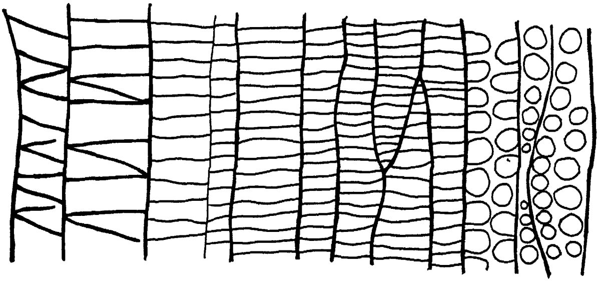


FIG. 3. *Callixylon Newberryi* (Dawson) Elkins & Wieland. Tangential section showing biseriation of rays. From Dawson's type section

PLATE XVI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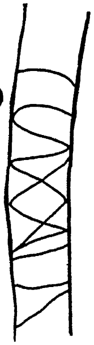
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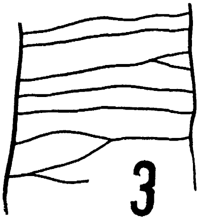
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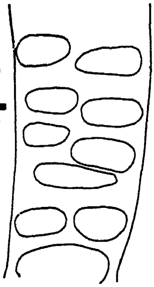
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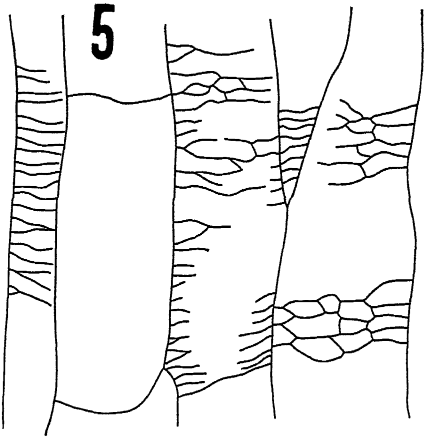
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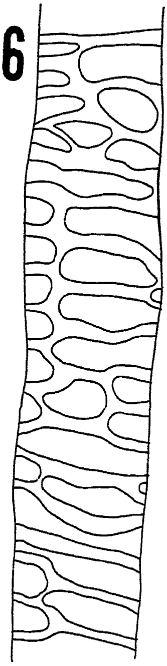

6

FIG. 1. *Dadoxylon Pedroi* Zeiller. Transition from scalariform to pitted structure in primary wood. From Seward, after Zeiller

FIG. 2–6. *Callixylon Zalesskyi* Arnold, sp. nov. Primary wood elements showing the various types observed in the transition from spiral to pitted structure. × about 570

PLATE XVII

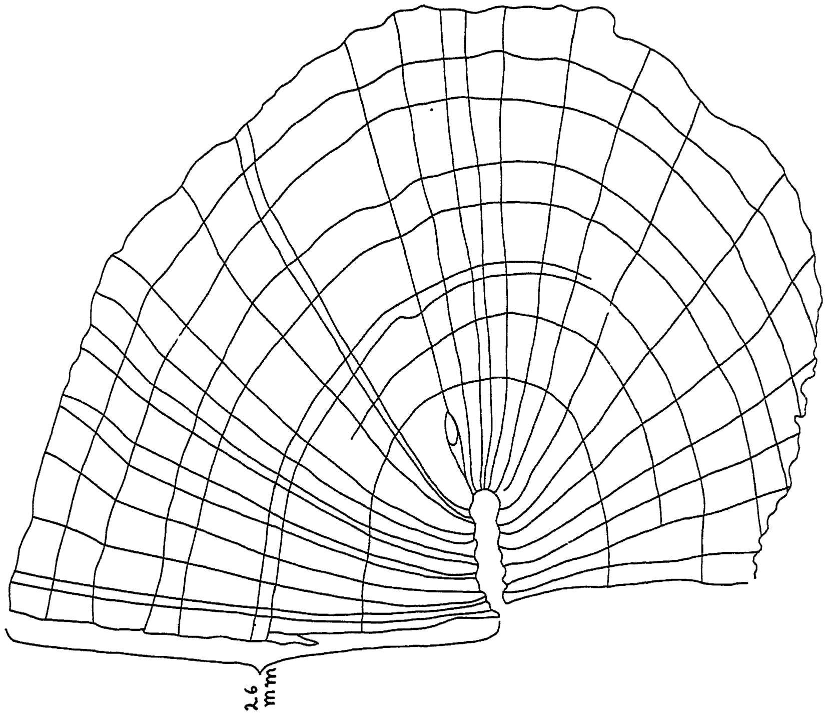


FIG. 1. *Callixylon erianum* Arnold, sp. nov. Diagram of one-half of stem showing spacing of growth rings. Two incomplete rings are also shown. × 2½

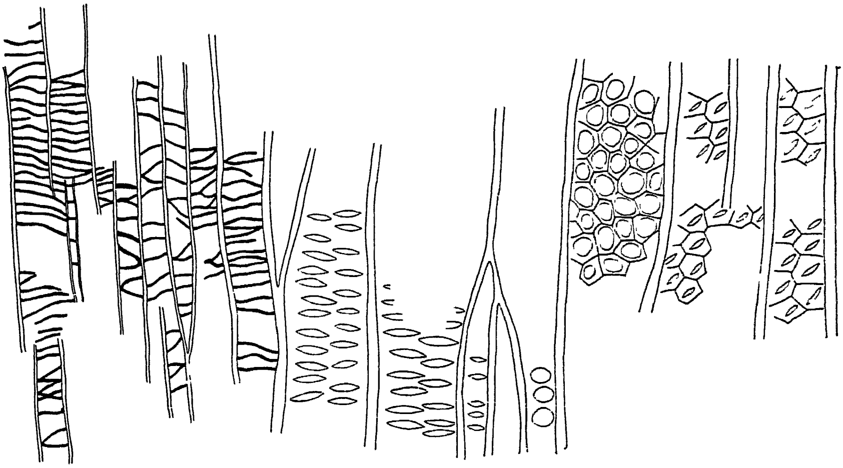


FIG. 2. *Callixylon erianum* Arnold, sp. nov. Complete radial section through primary wood bundle showing transition from annular to pitted structure. × about 60

PLATE XVIII

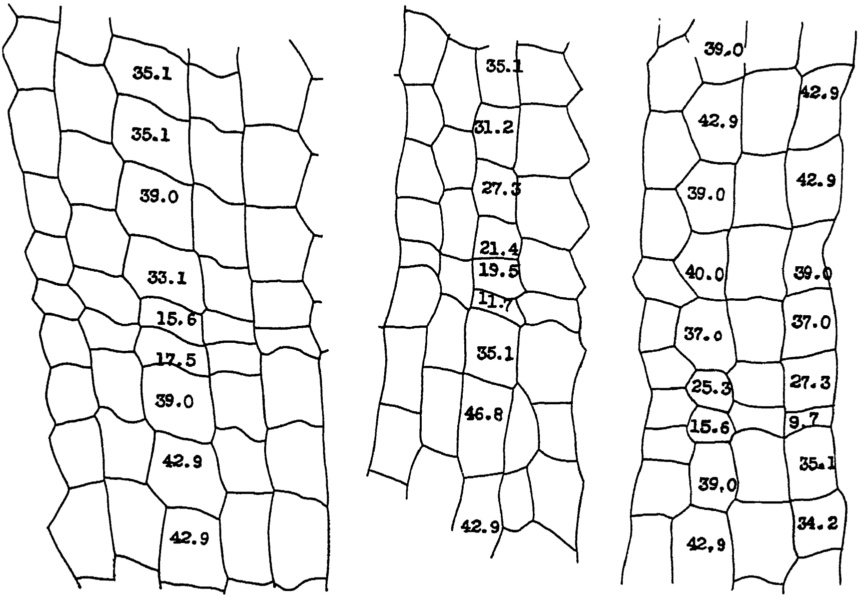


FIG. 1. *Callixylon sp.* Measurements showing gradual shortening of "summer" wood cells as outer boundary of growth ring is approached. The last "summer" wood cell is the shortest, then there follows an abrupt change in the succeeding layers of "spring" wood. × about 150

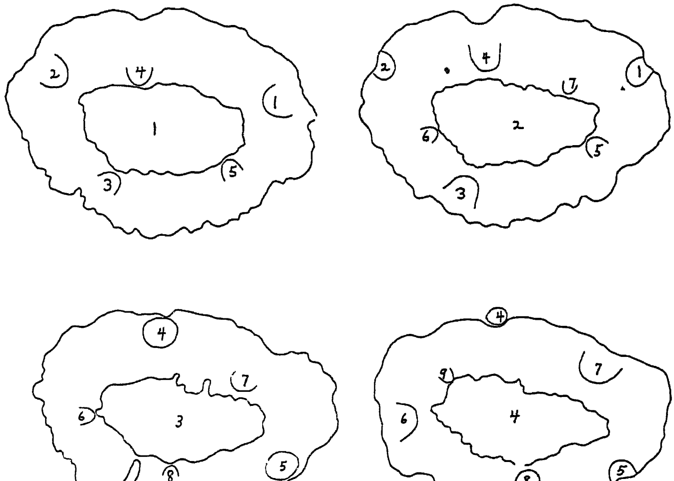


FIG. 2. *Callixylon Zalesskyi* Arnold, sp. nov. Series of sections from about three quarters of an inch of stem length showing the order of departure of the traces. × 2½

PLATE XIX

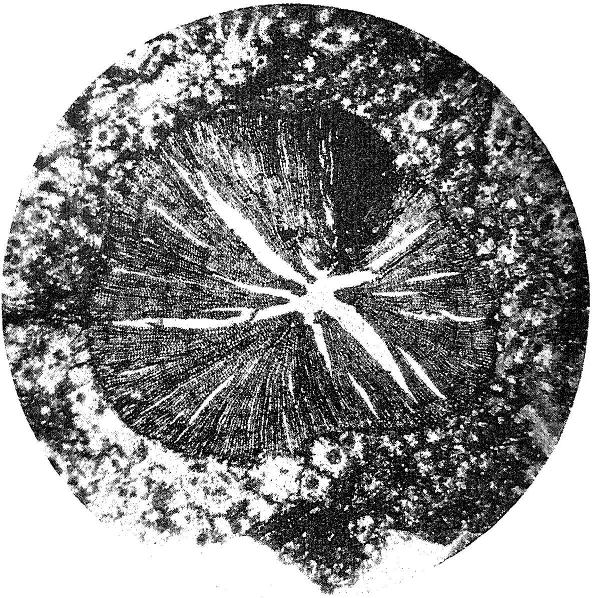


FIG. 1. Root of Callixylon. × 10

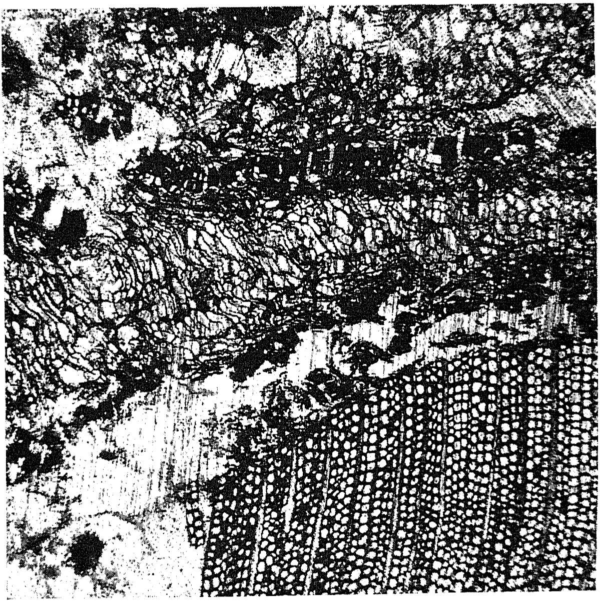


FIG. 2. *Callixylon Zalesskyi* Arnold, sp. nov. Portion of phloem. × about 35

THE FLORA OF TWO ACRES OF FARM LAND IN OAKLAND COUNTY, MICHIGAN

CECIL BILLINGTON

THE small parcel of Michigan farm land considered in this survey is now my summer place and is called "The Cove," from its situation on a cove of Lakeville Lake. It is located in Addison Township, Oakland County, about a quarter of a mile west of the village of Lakeville, on the Oxford Road, and extends from the highway to the south side of the lake. The property consists of approximately two acres of land, a portion of which is flooded by the lake, and was purchased from Mr. J. C. Townsend in the winter of 1921, after having been in the possession of the Townsend family for nearly seventy-five years. At the time of its purchase it was a pasture field and Mr. Townsend informs me that it was cleared and under cultivation when it came into the possession of his grandfather in 1855. Just how long previous to this the forest was cut away and cultivation started is not definitely known, but it is safe to say that it was nearly a hundred years ago. I secured the property with the idea of building a summer cottage and reforesting the entire piece, which has since been done.

It occurred to me that it might be interesting to see how many species of plants might be found growing on a piece of land which had been under cultivation for so long a period. In this particular case, of course, the number is increased by the addition of the shore plants and aquatics, but for the most part the list includes plants which might be found growing on any similar section of farm land having an old fence row. The survey was begun in 1922 and has been carried on each summer since, with scrupulous care used to include only plants found growing without special introduction within the limits of the area.

The reason for the inclusion of the aquatics in the list of species is the fact that Lakeville Lake is not a natural lake, but was formed by the construction of a dam for water-power purposes, thus flooding about a dozen small lakes and swamps and the surrounding land. This was done in 1830 after the land had been surveyed and consequently ownership of land extends under the water.

Practically the entire area of The Cove is a hillside with a northern exposure (Pl. XX, Fig. 1). The highest point is at the highway near the center of the property and is approximately sixty feet above the lake. From this point the land slopes gently to the east and west and, in places, rather abruptly toward the north, so that there is practically no level ground. The soil is the gravelly-clay-sand mixture, with numerous boulders typical of the morainic formations of this section of Michigan. The slope of the land has caused excessive erosion and the soil on the steeper parts of the hillside is very poor, almost incapable of supporting vegetation, so that in spite of our best efforts at seeding there are still many barren spots. As a consequence of the continual washing of the top-soil from the hillsides, the soil near the lake is very deep and rich and in places supports an almost impenetrable growth of brambles.

For slightly more than half its distance the bank of the lake rises abruptly from four to six feet and the rest slopes more gradually to the water. At the foot of the bank along the edge of the water *Carex stricta* is growing in abundance, forming large "stools" in which the redwing blackbird loves to nest. Where the land slopes gradually to the water there is an area of low, wet ground forming a most suitable habitat for other sedges and swamp plants, and here grows a large colony of sweet-flag.

Along the entire eastern side of the property there is an old snake rail fence, and in this feature lies the chief interest of the survey. Because it was not possible to plough close to it there remained in the fence corners a growth of trees, shrubs and plants of various kinds. It is here that the majority of the relict species of the forest days have taken refuge and have managed to persist during approximately a hundred years of the most adverse conditions of cultivation, pasturing and human depredation. It seems remarkable that such delicate plants as the wind-flower, *Anemone quinquefolia* (Pl. XX, Fig. 2), Oakesia and Maianthemum could so long hold out, but in the more shaded portions may be found colonies of all these plants, some in considerable numbers. Other relict deep-woods species such as *Smilacina racemosa, Sanicula marilandica, Viola scabriuscula, Amphicarpa monoica* and *Pedicularis canadensis* are sparingly represented. From the character of the surrounding soil and physical features of the land it may be supposed that parts of the original forest were of an "open, dry woods" nature. From these situations we have many other relict species which found a foothold and have persisted in the thickets and other uncultivated portions.

It is apparent from the evidence furnished by the old fence row that the oak was the dominant forest tree of this vicinity. With very few exceptions the trees belong to this genus. Of the four species listed the white oak is the most numerous, the red oak next, with the black and scarlet represented by only a few individuals each. The trees in the old fence row have now grown to considerable size and a deep-woods condition is again being created. It is hoped with the more suitable habitat the relict species growing there will again flourish and come into their own.

The road fence on the south was of the woven wire variety which permitted ploughing close to it. With the exception of one small oak tree there was no woody growth along it, and yet here in this most inhospitable situation were found a few plants of the common blue violet and of the wind-flower.

There were only two trees of any considerable size on the property at the time of its purchase. One was white pine about eighteen inches in diameter, located in the northeast corner near the lake. Under its protecting branches were found a number of deep-woods plants such as *Aster macrophyllus, Pedicularis canadensis, Viola conspersa, Amphicarpa monoica* and *Sanicula marilandica,* making the most of the only hospitable situation remaining to them outside the old fence row. The other was a black willow growing on the shore of the lake where the land slopes gradually to the water. Surroundng it in the deep, rich, moist soil there flourished a tangled mass of convolvulus, jewelweed and bedstraw.

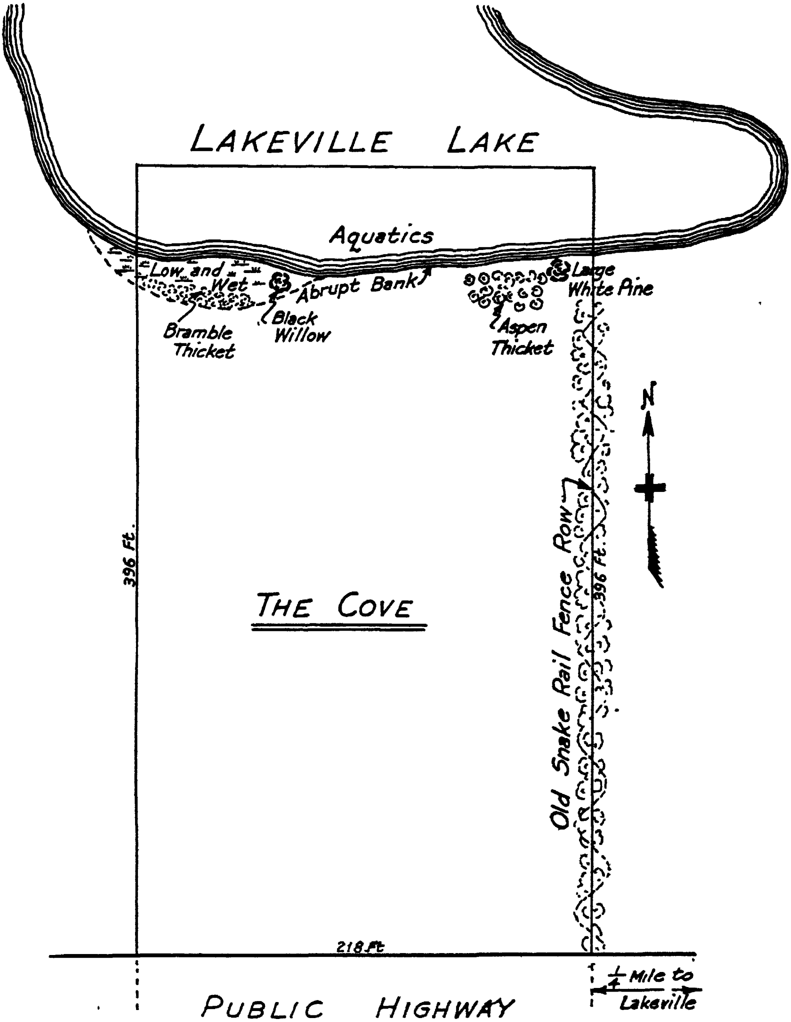
In the northeast corner on the bank of the lake there was a colony of about a dozen American aspens affording protection for a thicket of *Cornus paniculata.* In this situation also was found *Krigia amplexicaulis, Aster laevis, Aster umbellatus, Veronica virginica* and the only plant of wild columbine.

Cultivation of the land had stopped a little way back from the bank of the lake and this unploughed strip afforded a place for the growth of the common grasses and open ground plants and shrubs. Otherwise, the whole area had been cultivated and its flora for the most part was the usual relict species from this cultivation.

The arm of Lakeville Lake upon which The Cove is situated is narrow at this point and protected from prevailing winds by surrounding hills. On this account the water is usually calm and is never subject to very great agitation by the waves. This condition, coupled with the fact that the water is comparatively shallow and the lake bottom is a deep, black sludge, affords an ideal habitat for the growth of aquatic plants, and they have made the most of their opportunity (Pl. XX, Fig. 3). So thickly do they grow that in the summer months it is exceedingly hard to row a boat through them. The number of species is not large, but the tremendous number of individuals of each species makes up for this lack.

The accompanying sketch map (Map 2) indicates the area covered by the survey and its principal features. The list of species reveals only one rare find, *Cornus circinata.* It is more common northward, but I have found it but once before in this vicinity and that was about a mile away at the other end of Lakeville Lake. Two shrubs of it are growing in the old fence row about the middle of the hillside, and both bloomed and bore fruit during the summer of 1928. Beal's *Michigan Flora* states that it is "infrequent throughout."

The list is arranged according to Gray's *New Manual of Botany* (seventh edition) and contains fifty-nine families, one hundred and thirty-three genera, and two hundred and seventeen species and



MAP 2. Sketch map of "The Cove" showing the principal features affecting the flora

varieties. These species may be classified into three groups, as follows: (1) upland, (2) shore and marsh, (3) aquatic. The upland species may be subdivided into two classes, one group containing the species which might be expected to be found growing in this situation either as relicts of the original forest flora or because of having found suitable habitats in the uncultivated areas, and the other group those species which are growing as the result of cultivation of the land either as relicts or as weeds. To conserve space only the total number of species is given in each group, as follows:

	Species
Upland plants, natural distribution	114
Upland plants, resulting from cultivation	49
Shore and marsh plants	43
Aquatic plants	11
Total	217

Since many of the species were represented by only a few plants and some by only one, specimens taken were limited to just enough for identification purposes and do not make ideal herbarium sheets. On this account I have chosen to keep them in my own herbarium rather than to deposit them with the University of Michigan or Michigan State College.

ANNOTATED LIST OF SPECIES

POLYPODIACEAE (Fern Family)

Pteris aquilina L. — Brake or Bracken. Frequent in the old fence row and along the lake bank.

Aspidium Thelypteris (L.) Sw. — Marsh Shield-fern. Infrequent along the bank of the lake.

Onoclea sensibilis L. — Sensitive Fern. A few plants in low ground along the lake shore.

EQUISETACEAE (Horsetail Family)

Equisetum arvense L. — Common Horsetail. Far too abundant, being a most persistent and annoying weed in the low ground at the foot of the hill and defying our most strenuous efforts to eradicate.

EQUISETUM FLUIVATILE L. — Pipes. Wet ground along the lake shore.

EQUISETUM VARIEGATUM Schleich. var. NELSONI A. A. EATON. — Scattered along the bank near the lake and in cultivated portions.

PINACEAE (PINE FAMILY)

PINUS STROBUS L. —White Pine. One large tree in the northeast corner on the bank of the lake. The white pine undoubtedly constituted a considerable portion of the original forest of the vicinity, as there are many fine specimens in the woods near by.

SPARGANIACEAE (BUR-REED FAMILY)

SPARGANIUM EURYCARPUM Engelm. — Bur-reed. The dominant species in shallow water and wet ground along the shore of the lake.

NAJADACEAE (PONDWEED FAMILY)

POTAMOGETON NATANS L. — Abundant.

POTAMOGETON ZOSTERIFOLIUS Schumacher. — Abundant.

POTAMOGETON STRICTIFOLIUS Benn. — Abundant.

NAJAS FLEXILIS (Willd.) Rostk. & Schmidt. — Abundant along the shore in shallow water.

HYDROCHARITACEAE (FROG'S BIT FAMILY)

ELODEA CANADENSIS Michx. — Water-weed. Very abundant, in places filling the lake to the exclusion of all other vegetation.

GRAMINEAE (GRASS FAMILY)

ANDROPOGON FURCATUS Muhl. — Beard Grass. A few tufts on the hillside near the road.

DIGITARIA HUMIFUSA Pers. — Finger Grass. A few plants in open place at the top of the hill.

PANICUM CAPILLARE L. — Old-witch Grass. Abundant in cultivated ground.

SETARIA GLAUCA (L.) Beauv. — Foxtail, Pigeon Grass. Remaining too abundantly after cultivation.

CENCHRUS CAROLINIANUS Walt. — Sandbur. Along the public highway and spreading into the cultivated portions of The Cove.

LEERSIA ORYZOIDES (L.) Sw. — Rice Cut-grass. Abundant in damp ground along the lake shore.

MUHLENBERGIA FOLIOSA Trin. — Low places near the lake shore.

MUHLENBERGIA MEXICANA (L.) Trin. — Low places near the lake shore.

PHLEUM PRATENSE L. — Timothy. Abundant relict from former seeding.

AGROSTIS ALBA L. — Red Top. Abundant relict from former seeding.

CALAMAGROSTIS CANADENSIS (Michx.) Beauv. — Blue-joint Grass. Abundant along the lake shore.

POA COMPRESSA L. — Canada Blue Grass. Abundant in open cultivated portions.

POA TRIFLORA Gilib. — Fowl Meadow Grass. Plentiful on the banks of the lake and along the shore.

POA PRATENSIS L. — Kentucky Blue Grass. Abundant throughout the cultivated portions.

FESTUCA NUTANS Spreng. — Fescue Grass. A few plants in shaded portion of the old fence row.

CYPERACEAE (SEDGE FAMILY)

ELEOCHARIS PALUSTRIS (L.) R. & S. var. GLAUCESCENS (Willd.) Gray. — Spike Rush. Abundant in low ground along the lake shore.

SCIRPUS VALIDUS Vahl. — Great Bulrush. Abundant in shallow water along the lake shore.

SCIRPUS ATROVIRENS Muhl. — Low ground at the edge of the lake.

SCIRPUS CYPERINUS (L.) Kunth. — Wool Grass. Damp ground along the lake shore.

Carex scoparia Schkuhr. — Along the lake shore, scarce.

Carex trisperma Dewey. — Low damp ground along the lake, very rare.

Carex vulpinoidea Michx. — Abundant in low damp ground along the lake.

Carex stricta Lam. var. angustata (Boott.) Bailey. — Abundant at the foot of the bank along the lake shore.

Carex pennsylvanica Lam. — Abundant in wooded section of the old fence row.

ARACEAE (Arum Family)

Acorus Calamus L. — Sweet-Flag. One colony growing in low damp ground near the lake shore.

LEMNACEAE (Duckweed Family)

Lemna minor L. — Duckweed. Shallow water and quiet pools along the lake shore.

JUNCACEAE (Rush Family)

Juncus tenuis Willd. — Only a few plants in open sandy ground.

Juncus effusus L. — Common or Soft Rush. Damp ground along the shore of the lake, rare.

Luzula campestris (L.) DC. var. multiflora (Ehrh.) Celak. — Wood Rush. Shady portions of the old fence row.

Liliaceae (Lily Family)

Oakesia sessilifolia (L.) Wats. — A few plants in the wooded section of the old fence row.

Asparagus officinalis L. — Asparagus. A few plants scattered in the fence rows.

Smilacina racemosa (L.) Desf. — False Solomon's Seal. A few plants in the wooded portion of the old fence row and along the road fence.

Maianthemum canadense Desf. — One colony of perhaps a hundred plants in wooded section of the old fence row.

IRIDACEAE (IRIS FAMILY)

IRIS VERSICOLOR L. — Larger Blue Flag. A few clumps along the lake shore.

ORCHIDACEAE (ORCHIS FAMILY)

HABENARIA LACERA (Michx.) R. Br. — Ragged Fringed Orchis. Only one plant found in low ground near the lake.

SALICACEAE (WILLOW FAMILY)

SALIX NIGRA Marsh. — Black Willow. One tree on the lake shore. This and the white pine were the only trees of any size on the property.

SALIX DISCOLOR Muhl.—Glaucous Willow. One shrub on the lake shore.

SALIX PETIOLARIS Sm. — One shrub on the lake shore.

SALIX HUMILIS Marsh. — Prairie Willow. A few shrubs in the old fence row and in the aspen thicket.

POPULUS TREMULOIDES Michx. — American Aspen. A colony of about a dozen small trees in the northeast corner of the property on the bank of the lake.

POPULUS GRANDIDENTATA Michx. — Large-toothed Aspen. A few small trees in the old fence row.

JUGLANDACEAE (WALNUT FAMILY)

CARYA OVATA (Mill.) K. Koch. — Shag-bark Hickory. One small tree in the old fence row.

BETULACEAE (BIRCH FAMILY)

CORYLUS AMERICANA Walt. — Hazelnut. Several fruiting shrubs in the old fence row and along the bank of the lake.

FAGACEAE (BEECH FAMILY)

QUERCUS ALBA L. — White Oak. Several small trees in the old fence row.

Quercus rubra L. — Red Oak. Several small trees in the old fence row.

Quercus coccinea Muench. — Scarlet Oak. A few small trees in the old fence row.

Quercus velutina Lam. — Black Oak. A few small trees in the old fence row.

URTICACEAE (Nettle Family)

Boehmeria cylindrica (L.) Sw. var. scabra Porter. — Frequent in low ground along the lake shore.

POLYGONACEAE (Buckwheat Family)

Rumex crispus L. — Yellow Dock. The usual quota of this weed.

Rumex acetosella L. — Sheep Sorrel. Since the soil is poor, this plant flourishes throughout the portions that were under cultivation.

Polygonum aviculare L. var. vegetum Ledeb. — Infrequent in cultivated ground.

Polygonum lapathifolium L. — Only a few plants along the lake shore.

Polygonum amphibium L. — Abundant in shallow water along the lake shore.

Polygonum amphibium L. var. hartwrightii (Gray) Bissel. — In tall grass along the lake shore.

Polygonum Hydropiper L. — Water Pepper. Damp ground along the lake shore.

Polygonum acre HBK. — Water Smartweed. Low ground near the lake shore.

Polygonum Persicaria L. — Lady's Thumb. Damp ground along the lake shore.

Polygonum Convolvulus L. — Black Bindweed. Frequent in cultivated ground.

CHENOPODIACEAE (Goosefoot Family)

Chenopodium album L. — Lamb's Quarters, Pigweed. As usual, abundant in cultivated ground.

AMARANTHACEAE (AMARANTH FAMILY)

AMARANTHUS BLITOIDES Wats. — A frequent weed in cultivated portions.

CAROPHYLLACEAE (PINK FAMILY)

STELLARIA LONGIFOLIA Muhl. — Lake bank and the old fence row, frequent.

CERASTIUM VULGATUM L. — Common Mouse-ear Chickweed. A common weed in cultivated portions.

LYCHNIS ALBA Mill. — White Campion. At first a few plants in cultivated portion, now becoming abundant.

SILENE ANTIRRHINA L. — Sleepy Catchfly. Frequent in sandy, cultivated portions.

NYMPHAEACEAE (WATER LILY FAMILY)

NYMPHAEA ADVENA Ait. — Yellow Pond Lily. The dominant aquatic, growing so thickly in places that it is difficult to row a boat through them.

CASTALIA TUBEROSA (Paine) Greene. — Water Lily. Abundant in Lakeville Lake; a few plants growing at The Cove.

RANUNCULACEAE (CROWFOOT FAMILY)

RANUNCULUS CIRCINATUS Sibth. — Stiff Water Crowfoot. The water along the shore of the lake is thick with this species and at its flowering time gives the appearance of snow, so numerous are the blooms, and the air is heavy with their odor.

RANUNCULUS SCELERATUS L. — Cursed Crowfoot. Damp ground along the lake shore.

RANUNCULUS PENNSYLVANICUS L. f. — Bristly Crowfoot. Damp ground along the lake shore.

ANEMONE VIRGINIANA L. — A few plants scattered in the upland portions.

ANEMONE QUINQUEFOLIA L. — Wood Anemone, Wind-Flower. One colony of about a hundred plants in wooded portion of the old fence row; also a few plants along the road fence.

AQUILEGIA CANADENSIS L. — Wild Columbine. Only one plant in aspen thicket on the bank of the lake.

LAURACEAE (LAUREL FAMILY)

SASSAFRAS VARIIFOLIUM (Salisb.) Ktze. — Sassafras. Frequent in the old fence row; some of the shrubs have attained a height of fifteen feet or more.

CRUCIFERAE (MUSTARD FAMILY)

LEPIDIUM VIRGINICUM L. — Wild Peppergrass. Common weed in cultivated portions.

LEPIDIUM APETALUM Willd. — Abundant in cultivated portions.

SISYMBRIUM ALTISSIMUM L. — Tumble Mustard. Frequent in cultivated portions.

RADICULA PALUSTRIS (L.) Moench. var. HISPIDA (Desv.) Robinson. — Marsh Cress. A few plants along the lake shore.

ROSACEAE (ROSE FAMILY)

AMELANCHIER CANADENSIS (L.) Medic. var. BOTRYAPIUM (L. f.) T. & G. — Shad Bush. Two small trees in the old fence row.

CRATAEGUS ALNORUM Sarg. — One small shrub in the old fence row.

FRAGARIA VIRGINIANA Duchesne. — Strawberry. Large colonies in the old fence row and on the bank of the lake.

FRAGARIA VIRGINIANA Duchesne var. ILLINOENSIS (Prince) Gray. — Rich, open ground near the bank of the lake.

POTENTILLA MONSPELIENSIS L. — Occasional in open portions.

POTENTILLA CANADENSIS L. — Abundant in open portions.

RUBUS IDAEUS L. var. ACULEATISSIMUS (C. A. Meyer) Regel and Tiling. — Wild Red Raspberry. Abundant, forming dense thicket in rich soil along the bank of the lake; also in the fence rows.

RUBUS OCCIDENTALIS L. — Black Raspberry. A few bushes in the old fence row.

RUBUS ALLEGHENIENSIS Porter. — Wild Blackberry. Abundant in the old fence row.

RUBUS FRONDOSUS Bigel. — A few shrubs in the old fence row

RUBUS VILLOSUS Ait. —Dewberry. In fence rows and along the bank of the lake.

PRUNUS SEROTINA Ehrh. — Wild Black Cherry. Several medium-sized trees in the old fence row.

LEGUMINOSAE (PULSE FAMILY)

BAPTISIA TINCTORIA (L.) R. Br. — Wild Indigo. Only one or two plants in open place of the old fence row.

LUPINUS PERENNIS L. — Lupine. A few plants in open place of the old fence row.

TRIFOLIUM PRATENSE L. — Red Clover. Abundant relict from farm seeding.

TRIFOLIUM REPENS L. — White Clover. Abundant throughout.

TRIFOLIUM HYBRIDUM L. — Alsike Clover. Scattered in open places from farm seeding.

MELILOTUS ALBA Desr. —Sweet Clover. At first only a few plants, but becoming abundant.

MEDICAGO SATIVA L. — Alfalfa. An abundant relict from farm seeding.

MEDICAGO LUPULINA L. — Black Medick. Frequent in open places.

DESMODIUM NUDIFLORUM (L.) DC. — One plant in wooded section of the old fence row.

DESMODIUM CANADENSE (L.) DC. — Frequent in portions near the lake which had not been cultivated.

LESPEDEZA HIRTA (L.) Hornem. — A few plants in open place of the old fence row.

LESPEDEZA CAPITATA Michx. — A few plants on the hillside near the road.

AMPHICARPA MONOICA (L.) Ell. — Hog Peanut. Infrequent in wooded portion of the old fence row; also under the large white pine.

OXALIDACEAE (WOOD SORREL FAMILY)

OXALIS STRICTA L. — Abundant in open sandy portions.

OXALIS CORNICULATA L. — Lady's Sorrel. Frequent in open ground.

GERANIACEAE (Geranium Family)

Geranium maculatum L. — Wild Cranesbill. Scattered throughout the old fence row.

POLYGALACEAE (Milkwort Family)

Polygala polygama Walt. — A very few plants on the open hillside.

Polygala verticillata L. — A few plants in uncultivated ground near the lake.

EUPHORBIACEAE (Spurge Family)

Euphorbia maculata L. — Milk Purslane. Frequent in cultivated portions.

Euphorbia corollata L. — Flowering Spurge. A few plants along the road and bordering the old fence row.

ANACARDIACEAE (Cashew Family)

Rhus typhina L. — Staghorn Sumach. Old fence row. Flourishes in gravelly soil and is abundant in this vicinity.

ACERACEAE (Maple Family)

Acer saccharum Marsh. — Hard Maple. There is a row of large hard maples along the highway and from their seeds thousands of seedlings spring up all over The Cove.

BALSAMINACEAE (Touch-me-not Family)

Impatiens biflora Walt. — Jewelweed. Abundant in low ground along the lake shore, particularly under the large black willow.

VITACEAE (Vine Family)

Psedera quinquefolia (L.) Greene. — Virginia Creeper, Woodbine. Growing along the highway, abundant in this vicinity.

Vitis vulpina L. — River-bank or Frost Grape. Climbing on trees in old fence row. Very abundant in this vicinity where it makes itself a nuisance to the farmer. Noted old stems an inch or more in diameter which had been cut off in an effort to eradicate it.

MALVACEAE (MALLOW FAMILY)

MALVA ROTUNDIFOLIA L. — Common Mallow, Cheeses. Frequent weed in the cultivated portions.

CISTACEAE (ROCKROSE FAMILY)

LECHEA VILLOSA Ell. — Pinweed. Only a few plants on the open, sandy hillside.

VIOLACEAE (VIOLET FAMILY)

VIOLA SORORIA Willd. — Common Blue Violet. A half dozen or so plants along the road fence at the top of the hill.

VIOLA SCABRIUSCULA Schwein. — Smooth Yellow Violet. Abundant in wooded portions of the old fence row.

VIOLA CONSPERSA Reichenb. — A few plants making a last stand in damp, shaded ground under the large pine tree.

ONAGRACEAE (EVENING PRIMROSE FAMILY)

EPILOBIUM ADENOCAULON Haussk. — Willow-herb. Frequent in low, damp ground along the lake shore.

OENOTHERA MURICATA L. var. CANESCENS (T. & G.) Robinson. — Only a few plants in cultivated portions.

OENOTHERA BIENNIS L. — Common Evening Primrose. A frequent weed in cultivated portions.

HALORAGIDACEAE (WATER MILFORD FAMILY)

MYRIOPHYLLUM SPICATUM L. — Water Milfoil. Very abundant in deeper portions of lake.

ARALIACEAE (GINSENG FAMILY)

ARALIA NUDICAULIS L. — Wild Sarsaparilla. Abundant in the old fence row.

UMBELLIFERAE (Parsley Family)

Sanicula marilandica L. — A few plants in the wooded section of the old fence row and under the large pine tree.

Cicuta maculata L. — Water Hemlock. Frequent in wet ground along the lake shore.

Cicuta bulbifera L. —Frequent in wet ground along the lake shore.

Daucus Carota L. — Wild Carrot. Fortunately only a few plants in cultivated portion.

CORNACEAE (Dogwood Family)

Cornus circinata L'Her. —Round-leaved Dogwood. Two shrubs about the middle of the hill in the old fence row; very rare in this vicinity.

Cornus stolonifera Michx. —Red-osier Dogwood. Several large shrubs on the shore of the lake; also in the old fence row and along the road.

Cornus paniculata L'Her. — Paniculate Dogwood. Abundant; forming a thicket in the aspen colony, and scattered along the lake bank and in the fence rows.

PRIMULACEAE (Primrose Family)

Lysimachia quadrifolia L. — Frequent in wooded portion of the old fence row.

Lysimachia thyrsiflora L. — A few plants in low, wet ground near the lake.

APOCYNACEAE (Dogbane Family)

Apocynum androsaemifolium L. — Spreading Dogbane. Scattered in the old fence row and bordering the aspen thicket.

ASCLEPIADACEAE (Milkweed Family)

Asclepias tuberosa L. — Butterfly-weed. A few plants at the top of the hill near the road.

Asclepias incarnata L. — Swamp Milkweed. Frequent in wet ground along the lake shore.

Asclepias syriaca L. — Common Milkweed. Too plentiful in the cultivated portions.

CONVOLVULACEAE (Convolvulus Family)

Convolvulus sepium L. — Hedge Bindweed. Abundant in low ground along the lake shore, climbing over the shrubs in a smothering mass, particularly under the large black willow.

BORAGINACEAE (Borage Family)

Lithospermum arvense L. — Corn Gromwell. Frequent weed in cultivated portions.

VERBENACEAE (Vervain Family)

Verbena hastata L. — Blue Vervain. A few plants in open uncultivated portions.

LABIATAE (Mint Family)

Scutellaria galericulata L. — Skullcap. Occasional in low ground along the lake shore.

Nepeta Cataria L. — Catnip. In the old fence row and along the lake bank, infrequent.

Prunella vulgaris L. — Heal-all, Self-heal. Abundant in low ground toward the lake and in the old fence row.

Leonurus Cardiaca L. — Common Motherwort. Infrequent in the old fence row.

Monarda mollis L. — Horse Mint. Abundant in uncultivated portion toward the lake.

Lycopus rubellus Moench. — Frequent in low ground along the lake shore.

Lycopus americanus Muhl. — Frequent in low ground along the lake shore.

Mentha arvensis L. var. canadensis (L.) Briquet. — Canada Mint. Infrequent, in low ground along the lake shore.

SOLANACEAE (NIGHTSHADE FAMILY)

SOLANUM DULCAMARA L. — Bittersweet. Low places near the lake and in the old fence row, both the white- and purple-flowered forms being abundant.

PHYSALIS HETEROPHYLLA Nees. — Ground Cherry. Abundant in cultivated ground.

SCROPHULARIACEAE (FIGWORT FAMILY)

VERBASCUM THAPSUS L. — Common Mullein. A few scattered plants in open portions.

VERONICA VIRGINICA L. — Culver's-root. A few plants in the old fence row and in the aspen thicket.

PEDICULARIS CANADENSIS L. — Wood Betony, Common Lousewort. A few plants under the large pine tree and in the old fence row.

PLANTAGINACEAE (PLANTAIN FAMILY)

PLANTAGO RUGELII Duchesne. — A few scattered plants in open places.

PLANTAGO LANCEOLATA L. — English Plantain. Too abundant throughout the open portions.

PLANTAGO ARISTATA Michx. — "Thick as hair on a dog" throughout. Evidently a heavy infestation from farm seeding.

RUBIACEAE (MADDER FAMILY)

GALIUM APERINE L. — Bedstraw, Cleavers, Goose Grass. Growing luxuriantly in low ground along the lake shore and in the old fence row.

GALIUM BOREALE L. — Northern Bedstraw. Abundant along the lake shore bank; also in the old fence row.

CAPRIFOLIACEAE (HONEYSUCKLE FAMILY)

LONICERA GLAUCESCENS Rydb. — Honeysuckle. Only one plant in the old fence row.

Sambucus canadensis L. — Common Elder. Frequent in the old fence row and in rich ground along the lake shore, where it flourishes.

LOBELIACEAE (Lobelia Family)

Lobelia spicata Lam. — Only a few plants; low ground near the lake shore.

COMPOSITAE (Composite Family)

Eupatorium perfoliatum L. — Boneset. Infrequent, low ground along the lake shore.

Solidago hispida Muhl. — Only a few plants in shaded portion of the old fence row.

Solidago speciosa Nutt. — A few plants in open space of the old fence row.

Solidago juncea Ait. — Early Goldenrod. Probably the most abundant species at The Cove, growing in the greatest profusion throughout.

Solidago juncea Ait. var. ramosa Porter & Britton. — Well scattered throughout open ground, but not as numerous as the type.

Solidago nemoralis Ait. — Frequent in sandy open places.

Solidago canadensis L. var. gilvocanescens Rydb. — Well scattered along the bank of the lake and in the fence rows.

Solidago altissima L. — One large colony on the bank of the lake.

Solidago serotina Ait. — Growing luxuriantly in rich ground bordering the bramble thicket on the bank of the lake.

Solidago graminifolia (L.) Salisb. — Abundant throughout in open portions.

Aster macrophyllus L. — A few plants under the large pine tree.

Aster azureus Lindl. — Only one plant found in uncultivated ground border of the old fence row.

Aster cordifolius L. — A few plants in the old fence row.

Aster sagittifolius Wedemeyer. — A few plants scattered in open places.

ASTER LAEVIS L. — Frequent; border of the old fence row and in the aspen thicket.

ASTER LATERIFLORUS (L.) Britton. — Only one plant found near the highway.

ASTER UMBELLATUS Mill. — Several plants on the lake bank and in the aspen thicket.

ERIGERON PHILADELPHICUS L. — Fleabane. All the fleabanes growing in the greatest abundance throughout the cultivated portions; relict species from former hayfields.

ERIGERON RAMOSUS (Walt.) BSP. — Daisy Fleabane.

ERIGERON CANADENSIS L. — Horse-weed, Butter-weed.

ANTENNARIA FALLAX Greene. — Frequent in dry open portions.

ANTENNARIA NEODIOICA Greene. — One colony at the top of the hill in open ground.

GNAPHALIUM POLYCEPHALUM Michx. — Common Everlasting. A few plants scattered in the open upland portions.

AMBROSIA ARTEMISIIFOLIA L. — Rag-weed. No matter how poor the soil this weed seems to flourish.

RUDBECKIA HIRTA L. — Black-eyed Susan. An abundant relict species from former hayfields.

HELIANTHUS DIVARICATUS L. — Sunflower. Occasional in the old fence row.

BIDENS FRONDOSA L. — Beggar-ticks. Abundant in cultivated portions and along fences.

BIDENS CONNATA Muhl. — Swamp Beggar-ticks. Damp ground along the lake shore.

BIDENS CERNUA L. — Stick-tight. Damp ground along the lake shore. During one season of low water this and the preceding species formed a dense growth along the entire water's edge, indicating that the seeds were lying dormant in the soil under the water only awaiting an opportunity to sprout and grow as soon as the water receded.

ACHILLEA MILLEFOLIUM L. — Common Yarrow. Abundant in open portions.

ANTHEMIS ARVENSIS L. var. AGRESTIS (Wallr.) DC. — Corn Chamomile. Infrequent; open cultivated ground.

ARCTIUM MINUS Bernh. — Common Burdock. Fortunately only a few plants in the old fence row and in the low ground along the lake.

CIRSIUM DISCOLOR (Muhl.) Spreng. — Common Thistle. Only a few plants in open places.

CIRSIUM ARVENSE (L.) Scop. — Canada Thistle. Happily only a few plants.

KRIGIA AMPLEXICAULIS Nutt. — Cynthia. Frequent in open places in the old fence row and in the aspen thicket.

TARAXACUM OFFICINALE Weber. — Common Dandelion. Strangely only a few plants in the cultivated portions.

TARAXACUM ERYTHROSPERMUM Andrz. — Red-seeded Dandelion. Only a few plants in the old fence row.

LACTUCA SCARIOLA L. — Prickly Lettuce. Common in cultivated ground.

LACTUCA CANADENSIS L. — Wild Lettuce. A few plants in an open place in the old fence row.

LACTUCA HIRSUTA Muhl. — Only one plant; border of the old fence row.

LACTUCA VILLOSA Jacq. — Plentiful along the lake bank and in the old fence row.

PRENANTHES ALBA L. — Rattlesnake-root. Abundant in wooded section of the old fence row.

HIERACIUM CANADENSE Michx. — One plant in open section of the old fence row.

DETROIT, MICHIGAN

PLATE XX

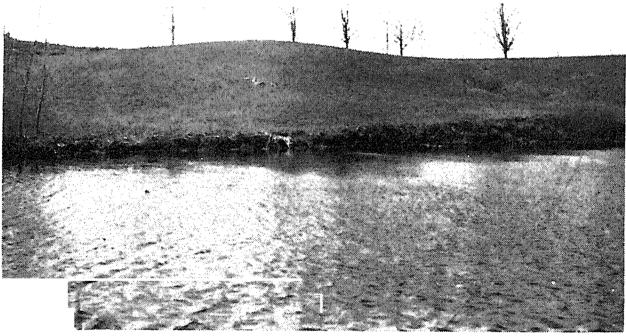


FIG. 1

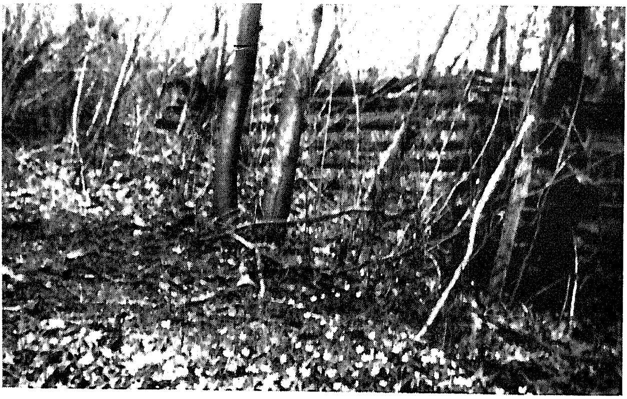


FIG. 2

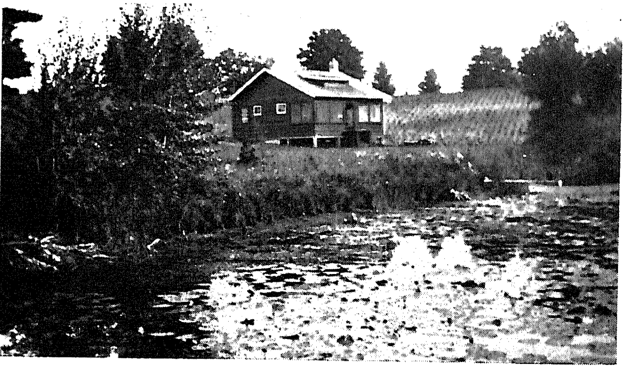


FIG. 3

EXPLANATION OF PLATE XX

FIG. 1. General view of "The Cove" April 16, 1922. This shows the property as ordinary farm land and as it looked when the survey of its flora was begun. A few trees of the aspen thicket may be seen on the lake bank. The old fence row does not show in this picture, but it is on the left (see Map 2).

FIG. 2. A section of the old fence row on the east side of "The Cove" showing a large colony of wind-flower, *Anemone quinquefolia.* This was probably the largest colony of relict forest species represented, although a colony of *Maianthemum canadense* near by had nearly as many plants. Photograph by John M. Sutton, May 8, 1927.

FIG. 3. View of "The Cove" showing the abundance of aquatic growth. The "stools" of *Carex stricta* along the foot of the lake bank may also be seen. A few branches of the large white pine mentioned in the text of the article may be seen at the left of the picture, as well as the black willow at the right. This view was taken July 2, 1922, after the cottage had been built.

THE PHYSIOLOGY AND VARIATIONS OF *CERCOSPORA BETICOLA* IN PURE CULTURE

GEORGE H. COONS AND FINLEY G. LARMER *

CERCOSPORA BETICOLA Sacc. is a cosmopolitan fungus causing leaf-spot of sugar beets and allied plants, such as the garden beet, mangold-wurzel, Swiss chard and other members of the family Chenopodiaceae. It is a common parasitic disease of the wild beet (*Beta maritima*) in Europe (5) and is sometimes found as a leaf-spot disease on a native plant (*Martynia louisiana*) of the central and western plains states which is a common weed in the beet fields of Colorado.

The disease is evidenced as small brown spots, with reddish-purple margins, which later become ashen-gray at the center owing to production of conidia. These spots are scattered irregularly over the surface of the leaf, but may become so numerous as to coalesce. In time, with severe infections, the leaf blade assumes a parched appearance, begins to discolor gradually from the distal portion toward the petiole, and finally becomes brown, crisp and somewhat curled or rolled. The outer or older leaves are the first to show these effects and wither away after the petioles wilt. To replenish this deficiency of leaf area the plant produces new leaves at the center of the crown. Consequently, the crown becomes elongated and with early infections the root remains abnormally small as the food reserves of the plant are consumed in replacement of leaf tissue rather than in growth and storage. As a result of the high crown, wasteful topping must be practised to eliminate certain organic salts that prevent the sugar from crystallizing after it has been extracted.

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* EDITORS' NOTE. — Mr. Larmer is the senior writer. The editors learned this too late to make the changes required in paging by a reversal of the order of the names.

Cercospora leaf-spot has long been recognized as being one of the most destructive foliage diseases of the sugar beet, but its importance has in some areas been minimized because with certain rainfall distribution its damage is small. The fungus never causes complete destruction of the plant, as happens with many of the root-rot fungi, or the deformities of the foliage that characterize the virus diseases, especially curly-top. Infection occurs in cycles, thus enabling the host partially to recover, so that the destructive effects on the growing plant are emphasized only in severe infections such as occur during wet seasons and in the irrigated regions where rainfall and excessive use of ditch water cause epidemic outbreaks.

Pool and McKay (9) have contributed most to our knowledge of the etiology of leaf-spot. They have correlated epidemics of leaf-spot with climatic conditions, primarily the influences of temperature, humidity and other environmental factors on the production and dissemination of conidia. Aside from the reports of various experiment stations on control measures, there is little other American literature dealing with *Cercospora beticola.*

This paper, which reports the results of studies of the reactions of the fungus to various cultural conditions, is divided into two parts: the first on the morphology, cultural characteristics and physiological reactions to environment of the normal fungus; the second on the abnormal or variant forms that it has produced.

PART I

METHODS

Leaf-spot material was obtained from the sugar-beet growing districts of Colorado, California, Minnesota, Iowa, Nebraska and Michigan, all of which are subject to outbreaks of the disease. Single-spore cultures were obtained by the dilution plate method; the individual conidia were marked as soon as germination could be detected by microscopic examination. The germinated spore in a minute block of agar was transferred to corn meal agar in test tubes and furnished the stock cultures used in the experimentation. Cultures were identified by microscopic examination, cultural characteristics, production of conidia, and sometimes by passage through plants, in which case the reisolation was compared with the stock culture. Cultural studies have been made from both test tube and petri dish cultures; plate cultures were used most extensively since they are more easily observed.

Sugar beets used in artificial inoculation work were grown in pots in the greenhouse and inoculated by spraying spore and mycelial suspensions upon the leaves. The plants were then placed under bell-jars and put in a temperature and humidity chamber, since moderately high temperature and humidity have been found to be most favorable for infection.

MORPHOLOGY OF THE ORGANISM

Mycelium. — The mycelium formed in pure culture varies greatly according to the food constituents of the medium. The young hyphae are hyaline and tubular, with thin walls and septa only at long intervals, and filled with a homogeneous, finely granulated cytoplasm. As they grow older they become greenish-brown, build heavier walls, and the cytoplasm becomes coarsely granular and filled with large, highly refractive, globular bodies which are soluble in ether. Septa are formed at short intervals and the mycelium often becomes gnarled, tortuous and irregular in shape. The aërial mycelium is usually more regular, somewhat smaller and less deeply colored, often almost hyaline. Sclerotium-like bodies composed of loosely massed hyphae are often observed in the submerged mycelium at the point of contact with the petri dish. These bodies appear to be formed by abnormal division and growth of a few cells and are more prevalent in newly isolated cultures. They resemble very closely the sclerotium-like bodies formed in the substomatal spaces of the leaf from which the conidiophores arise. Several of the masses, however, have been isolated and kept in distilled water and broth cultures, but fructification has never been observed.

Conidiophores. — Fructification under ordinary conditions in culture results in the production of abnormal conidiophores, Normal conidiophores are fasciculate, simple, erect and flavous.

arising from a few celled stroma in the substomatal cavity of the leaf. Under field conditions, conidiophores are normally short and non-septate, although septation and elongation into hypha-like structures may occur in the older conidiophores (XXI, Fig. 1). This latter condition is especially true on artificially inoculated plants grown under humid conditions in the greenhouse. The simple conidiophores may have one or two indistinct septa near the base. They vary from 35 to 80 microns in length, and have an average width of 4 to 5 microns. The older hypha-like conidiophores are sometimes as much as 180 microns long with septa 20 to 40 microns apart. In artificial cultures the younger conidiophores are short, simple and non-septate, arising directly from a submerged filament (Pl. XXI, Fig. 3). At the apical end is seen a distinct scar, circular in outline, which indicates the point of attachment of the spore. Older conidiophoes may have several of these scars along the surface with a geniculation at each scar. When a mature conidiophore with one spore is put under favorable conditions, it sends out new growth from just beneath the scar. From this new growth another conidium is produced and abscissed, leaving a distinct bend. The older conidiophores are long, septate and hypha-like, resembling the older structures found on plants. As the conidiophore begins to decline, conidium-like branches arise; these branches and the conidiophores serve as permanent hyphae (Pl. XXI, Fig. 2).

Conidia. — As a rule, conidia are typically obclavate to needle-shaped, hyaline and multiseptate, and show typical circular attachment scars. Abnormal conidia varying from structures consisting of one or two cells to extremely long, multiseptate, hypha-like filaments are sometimes produced (Pl. XXI, Figs. 4–6). Conidia measured from normal cultures had a maximum length of 260 microns and a minimum length of 55 microns; the average length was 140 microns, and the average number of septa per conidium 10.8. The spore contents are finely granular, non-vacuolated and practically hyaline; conidia produced in pure culture are slightly more transparent than those produced on sugar beets.

CULTURAL CHARACTERISTICS

Many kinds of media have been used in the study of the fungus since a careful delineation of the cultural characteristics of the organism on artificial media is needed to furnish ready means for its identification. This work has also given information concerning conidial production and various physiological phenomena of the organism, and, as will be indicated by the work presented later, certain variants depart strongly from the normal behavior of the species.

Growth on media. — The fungus was found to grow well on most of the thirty different media employed, but corn meal agar and beet leaf agar[1] are the only two worthy of special mention here, the first as a differential medium, since it has been found to produce a very characteristic vegetative growth, and the second for its value in the study of spore production in artificial culture. On corn meal agar the fungus produces a characteristic olive-green colony[2] with greenish-gray, aërial mycelium. *Alternaria sp.* is sometimes obtained as a contamination in dilution plate isolations of *beticola* from sugar beet leaves, but is readily recognized by the conidia which are produced in abundance on this medium.

Influence of depth of medium and amount of nutrients. — In order to determine the effects of the depth of medium and quantity of nutrients upon the organism, the following tests were carried out. Petri dishes were supplied with 12 and 25 c.c. and deep culture dishes with 50 c.c. of the nutrient agars listed in Table I and inoculated with strain C-8. These factors, with the exception of the media containing aniline dyes, were found to have very little influence on breadth of growth.

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[1] Preparation of beet leaf agar:

1. Young sugar beet leaves dried at 40° C. and finely powdered.
2. 15 grams of beet leaf flour and 15 grams of agar agar cooked slowly in distilled water for 30 minutes.
3. Strained through cheese cloth and made up to 1000 c.c.
4. Autoclaved at 15° pressure for 20 minutes.

[2] In accordance with general usage in plant pathology, the so-called "pseudo-colony" of a fungus is termed a "colony."

TABLE I

INFLUENCE OF DEPTH OF MEDIUM ON LINEAR GROWTH OF *C. beticola*

Values represent diameter of colony growth in millimeters

Agar medium	12 c.c.		25 c.c.		50 c.c.	
	Days of growth					
	10	20	10	20	10	20
Oatmeal........	17	62	18	63	18	70
Litmus lactose...	19	27	18	49	18	50
Potato dextrose..	20	70	19	69	22	72
Bean pod.......	19	64	18	70	21	70
Corn meal......	20	62	20	76	20	69
Malt extract....	22	67	25	82	19	80
Beet leaf.......	19	55	18	48	18	42
Plain...........	17	61	18	69	18	66
Coons' synthetic.	25	82	25	80	23	80
Neutral red.....	12	24	10	36	11	36
Prune juice.....	20	74	21	76	19	68
Lima bean......	21	71	17	68	19	76
Endo's.........	14	39	14	45	15	45
Average....	19.6	59	18.5	64	18.5	62

Observations on density and amount of mycelial growth were made after twenty days, at which time the mycelium had attained the greatest depth in the 50 c. c. plates, and was profuse and matted. The abundance of food did not affect linear extent of surface growth, but permitted further growth after the first ten days, giving greater density to the colony.

Light relations. — It is evident from the data given in Table II that light relations are not very marked on the growth of the fungus. These findings are similar to those of Klotz (8) in respect to *Cercospora apii*, a closely related species. Growth on corn meal agar was abundant and matted in all forms under the different conditions, differing only in the color of the mycelium, which was grayish-white under continuous light, light greenish-gray under diurnal light, and dark greenish-gray in continuous darkness.

Growth was more rapid on potato dextrose agar, but the color contrast was lacking, all cultures having light greenish-gray aërial mycelium. Observations made at different times showed only a difference in color of mycelium between cultures grown in light and darkness; cultures in light were somewhat lighter colored.

TABLE II

GROWTH OF *C. beticola* IN RELATION TO LIGHT

Condition of growth	Temperature	Medium	Strain	Colony diam. mm.			
				Days of growth			
				2	6	10	14
Darkness	22°–24° C.	Potato dextrose agar	C–11				42
			C–13				45
			C–23				43
		Corn meal agar	C–11				26
			C–13				25
			C–23				27
Ordinary daylight conditions	21°–23° C.	Potato dextrose agar	C–11	2	13	24	36
			C–13	2	17	31	42
			C–23	2	15	26	38
		Corn meal agar	C–11		9	17	22
			C–13		11	20	27
			C–23		12	20	26
Light from 100 watt nitrogen filament bulb	24°–25° C.	Potato dextrose agar	C–11	2	16	29	40
			C–13	2	16	27	38
			C–23	2	14	25	36
		Corn meal agar	C–11		11	21	25
			C–13		10	19	24
			C–23		11	20	24

Data on the effect of light on conidial production are tabulated in Table III. The cultures were grown on 18 c. c. of beet leaf agar in a 250 c. c. flask for a ten-day period. Washings from the cultures showed that conidia were produced most abundantly under ordinary diurnal conditions. This will probably explain the slightly slower linear growth as being due to checking of the mycelial filaments resulting in conidial formation under fluctuating light.

TABLE III

THE EFFECT OF LIGHT ON CONIDIAL PRODUCTION IN *C. beticola* GROWN IN FLASKS ON BEET LEAF AGAR

Numerical values represent diameter of growth in mm.; all spores produced were apparently normal in type. Cultures illuminated by 100 watt nitrogen-filament bulb.

Strain	Light 24–25° C.	Daylight 21–23° C.	Darkness 22–24° C.
	Growth	Growth	Growth
C–11	24	22	27
C–11	25	21	27
C–13	26	22	24
C–13	26	23	25
C–23	24	24	25
C–23	24	24	24
Average	25.8	23.2	25.3

Temperature relations. — The occurrence of epidemics of Cercospora leaf-spot during the late summer months would indicate that high temperatures are necessary for optimum development of the fungus. A nine-compartment differential thermo-regulator was employed in studying the relation of temperature to growth of the organism. Inoculum from corn meal agar cultures of strains C–11, C–13 and C–23 was transferred in duplicate to 15 c. c. of agar in petri dishes and incubated for a period of ten days, when the data were taken. Since there were only slight differences between strains on a given medium, the data have for simplicity and convenience been averaged and are recorded thus for each temperature range (Table IV).

These data indicate that the fungus grows well between 20° and 30° C.; temperatures above or below these limits are detrimental to the best growth of the organism. The optimum temperature as determined by the size and the color of the mycelium is around 24–26° C. Good growth takes place below the optimum, but with a gradual decline in rate of growth. Temperatures above the optimum seem to stimulate abnormal growth; the organism becomes pale and produces considerable aërial mycelium.

TABLE IV

THE EFFECTS OF TEMPERATURE ON GROWTH OF *C. beticola*

Compartment	Temp. range	Medium (agar)	Colony diam. mm.			Character of growth
			Max.	Av.	Min.	
1	6–10° C.	Corn m.				Too slight to measure
		Nutrient				do.
		Pot. dex.				do.
2	14–16° C.	Corn m.	7	6	5	Poor, deep olive green
		Nutrient	11	9	4	do.
		Pot. dex.	15	10	4	do.
3	17–18° C.	Corn m.	16	14	13	Fair, green, aërial slight
		Nutrient	18	15	13	Fair, mouse gray, slight
		Pot. dex.	19	17	15	Fair, greenish-gray, slight
4	19–21° C.	Corn m.	20	18	16	Good, deep olive green
		Nutrient	18	17	13	Good, dark gray
		Pot. dex.	26	24	22	Good, greenish-gray
5	22–23° C.	Corn m.	18	15	14	Like (4)
		Nutrient	16	15	14	Like (4)
		Pot. dex.	28	26	24	Like (4), slightly better
6	24–26° C.	Corn m.	28	23	20	Optimum, like (4) in color
		Nutrient	18	16	14	do.
		Pot. dex.	30	28	27	do.
7	27–29° C.	Corn m.	32	25	20	Profuse, pale growth
		Nutrient	15	15	14	Profuse, white aërial growth
		Pot. dex.	32	30	30	Profuse, white and felty
8	32–34° C.	Corn m.	14	9	8	Poor, aërial pale, heavy
		Nutrient	7	6	6	Poor, white throughout
		Pot. dex.	15	9	3	Poor, aërial white, heavy
9	37–40° C.	Corn m.				No growth
		Nutrient				do.
		Pot. dex.				do.

Pool and McKay report that conidial production on the host plant is greatly influenced by temperature and humidity. Duplicate transfers of strains C–11, C–13 and C–23 were made on beet leaf agar in petri dishes and incubated at the various temperatures of the thermo-regulator for ten days (Table V). Heaviest sporulation was found to occur at the lower limits of temperature for optimum vegetative growth of the fungus, but conidia are produced to some extent over a temperature range of 17–29° C. High temperature stimulates linear growth, conidia often exceeding 260 microns, while short, robust spores with few septa are characteristic of low temperature.

TABLE V

THE EFFECTS OF TEMPERATURE ON CONIDIAL PRODUCTION IN CULTURES OF *C. beticola*

Compartment	Temp. (° C.)	Colony diam. mm.			Character of growth	Spores
		Max.	Av.	Min.		
1	6–10				None	None
2	14–16	7	6	5	Poor	None
3	17–18	14	13	11	Fair	+ short, robust
4	19–20	20	18	16	Good	++ typical
5	22–23	20	18	13	Good	+++ typical
6	24–26	23	19	15	Optimum	+++ longer than in (5)
7	27–29	22	19	15	Abnormal	+ few and long
8	32–34	14	10	5	Poor	Few and hypha-like
9	37–40				Death	None

Formation and germination of conidia. — Conidial production on artificial media has never been reported in any of the literature reviewed, although it has been known to occur in other members of the genus Cercospora (6, 8). Typical conidia have been found on beet leaf agar and more or less normal spores have since been found on several media. Such instances, however, are rare and the conidia are so abnormal that they could be readily overlooked. Description of these conidiophores and conidia has been given and compared with those produced on plants in a previous section ("Morphology of the organism").

Conidia produced in artificial cultures germinate in the usual manner (Pl. XXI, Fig. 5). The end cells germinate first, sending out long, slender, hyaline, sometimes branching germ tubes, with the intermediate cells germinating shortly afterwards. It is seldom that more than 50 per cent of the conidial cells germinate; some desiccation of the non-viable cells apparently takes place. Infection on sugar beets can be produced as readily with these conidia as with conidia produced on the plant.

Spores are produced over the entire surface of the mycelial growth, but they are seen in greatest numbers at the borders of the colony, owing probably to the formation of hypha-like conidiophores and the abscissing of the conidia. Heavy fructification on beet leaf agar is indicated by a dark olive green to black mycelium in the substratum, with sparse aërial growth which is dark, short and mealy. There is a tendency for cultures to lose their power of conidial production when grown in artificial cultures continuously for long periods. Loss of vegetative vigor and color are generally indicative of partial sterility. Achromatic cultures resulting as gradual or sudden variations are almost invariably sterile, although conidia much smaller than normal have been observed in a few instances. Heavy aërial mycelium is usually accompanied by low conidial production.

From the data given the conclusion can be drawn that conidial production in artificial cultures of *C. beticola* is a response to a food stimulus influenced more or less by other factors such as humidity, light and temperature.

Loss of color.—Loss of the characteristic green color through reduction in the amount of greenish-brown pigment in the mycelium has occurred commonly when the fungus has been kept in culture on artificial media for long periods. Factors which seem to influence this phenomenon are high temperatures, desiccation in old cultures and quality and quantity of nutrients. None of the factors when tried experimentally have induced permanent loss of color. Cultures grown at high temperatures have given pale, almost achromatic growths, which immediately became normal green when transfers were made from these cultures and normal conditions restored.

Observations on the effects of desiccation in relation to loss of color in subsequent transfers were made by taking inoculum from normal, olive-green cultures that had dried out with age. The following table shows the results of transfers made from the original stock culture of several forms, over different periods. Transfers were made on corn meal and potato dextrose agar slants and incubated at 25° C. for ten days before observations were made.

TABLE VI

VIABILITY OF *C. beticola* IN CULTURES

Strain	Age of culture	Transfer of 12/2/27		Transfer of 3/20/28	
		Corn meal agar	Potato dextrose agar	Corn meal agar	Potato dextrose agar
C-1	10/31/26	Normal	No growth	Normal	Normal
C-2	10/31/26	do.	Normal	do.	do.
C-3	10/31/26	do.	do.	do.	do.
C-4	11/1/26	do.	do.	do.	do.
C-5	11/1/26	do.	do.	do.	No growth
C-10	11/5/26	do.	do.	do.	Normal
C-11	11/5/26	do.	do.	do.	do.
C-13	11/5/26	do.	do.	do.	do.

These data show that only normal cultures were obtained from eighteen-month-old cultures that were completely dried out. Subtransfers from these cultures after they had grown for thirty days gave only normal forms with no indication of loss of color.

Certain nutrient media produce cultures that are pale green; this is particularly true of a 1.2 per cent washed, plain agar medium. Strains C-6 and C-17 were grown on plain agar medium and small quantities of inoculum were taken from the edge of the colony to obtain as near a homogeneous material as possible. This inoculum was transferred to petri dishes containing 15 c.c. of plain agar medium and allowed to grow for fifteen days when the cultures received the treatments indicated in Table VII.

TABLE VII

TREATMENT OF PALE CULTURES WITH AMINO ACIDS

Treatment	Strain C–6	Strain C–17
Leucine	No change	Same as C–6
Tyrosine	Greenish-black	do.
Alanine	New growth light green	do.
Glycine	No change	do.
Cystine	do.	do.
Asparaginic acid	New growth normal green	do.
Corn meal agar	Normal culture	do.
Check	No change	do.

This experiment was run in duplicate and repeated with similar results. It indicates that certain amino acids are available for the nutrient of the fungus and have a tendency to bring out the green pigment. Achromatic cultures of unknown origin and the aberrant form of strain C–1 have been treated similarly with negative results.

These data indicate that the abnormally pale forms studied are not of the same nature as those which are obtained through either continuous culture or the aberrant forms, in that they immediately return to the normal green color when grown under favorable conditions.

ZONATION

The formation of zones, i.e., production of concentric rings of light and dark mycelium, is a peculiarity exhibited by many fungi growing in artificial culture. Structural characteristics of the colony growth such as varying density and amount of spore massing, grouping of pycnidia and sclerotia, mycelial branching, color, and the like, due to differential growth, are largely responsible for the occurrence of this phenomenon. These effects have been attributed to various causal agencies, such as light and temperature relations, resting periods, staling products, mycelial crowding, alkaline medium and variations in the amount of nutrient. Stevens and Hall (12) emphasize the fact that zonation may be induced by fluctuation of the foregoing external factors, but that it is largely dependent upon the fungus.

Zonation in cultures of *C. beticola* is due, apparently, to differential rate of linear growth of the submerged mycelium. Microscopic examination shows that the dark bands are due to a large number of short, irregular and somewhat distorted filaments, while the light bands consist of a small number of long, smooth and regular filaments. It seems that in this fungus the dense crowding of the filaments resulting from their repeated branching inhibits growth resulting in a period of quiescence followed by the onward growth of a few of the more vigorous hyphae. The rapidity of succession of zones depends upon the relation existing between the rate of branching and the increase in linear growth which is controlled by some fluctuating external condition.

Of the external factors that might induce zonation, fluctuating light and temperature conditions were believed to be the most important, since there seemed to be a new zone formed each day, so the effects of these factors were observed under controlled conditions in the following experiments.

Data on zonation of *C. beticola* in relation to fluctuating light and different types of light are given in Table VIII. Twenty cubic centimeters of agar were poured into petri dishes of the same depth and diameter and plantings were made in each quadrant of the culture dish and incubated in chambers designed for studying light relations. Diffused daylight was admitted through a north exposure and red and blue lights by passing natural light from the same source through glass filters. Continuous light was furnished from a 110 volt–100 watt nitrogen filament bulb, as was the light for the 10- and 30-minute exposures. Observations were made after the culture had grown for twelve days.

With the same type of petri dishes and media prepared as described above, an attempt was made to determine the relationship of fluctuating temperatures and zonation in cultures of *C. beticola*. Plantings were made, the petri dishes carefully wrapped and incubated under the conditions outlined in Table IX. On repeating the experiment only corn meal and oatmeal agars were

TABLE VIII

EFFECT OF LIGHT ON ZONATION IN *C. beticola*

0 = No zonation
± = Zonation very faint
+ = Zonation pronounced

Agar medium	Daylight blue filter				Daylight red filter				Ordinary daylight conditions				Contin-uous* light				Continuous darkness				Darkness with light* exposures of							
																					10 min.				30 min.			
	1	8	20	27	1	8	20	27	1	8	20	27	1	8	20	27	1	8	20	27	1	8	20	27	1	8	20	27
Corn meal	+	+	+	+	0	0	0	0	+	+	+	+	0	0	0	0	±	±	±	±	±	±	±	±	+	+	+	+
Potato dextrose		+	+	+	0	0	0	0	+	+	+	+			0	0	0	0	0	0		0	0	0		+	+	+
Beet leaf	+	+	+	+	0	±	0	±	+	+	+	+		0	0	0	±	0	±		±	±	±	±	+	+	+	+
Oatmeal	+	+	+	+	0	±	0	±	+	+	+	+	0	0	0	0	±	±	±	±	+		+	+	+		+	+
Lima bean	+	+	+	+	0	0	0	0	+	+	+	+	0	0	0	0	0	0	0	0	0		0	0	+		+	+
Malt extract	+	+	+	+	0	0	0	0	+	+	+	+	0	0	0	0	0	0	0	0	0		0		+		+	
Prune juice		+	+	+	0	0	0	0	+		+	+		0	0	0		0	0	0		0	0	0		+	+	+
Plain	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

* Light from 100 watt nitrogen-filament bulb.

used, but more culture forms were employed. Sets A and C were kept as before, but set B was given different lengths of exposure to the various temperatures, i.e., five days at 24° C. and 12 hours at 12° C.; five days at 24° C. and 24 hours at 12° C.; and then five days at 24° C. before the observations in Table X were made.

A set of plates from the constant 24° C. chamber were kept under a bell-jar in the laboratory for two weeks after this experiment was completed. They were exposed to daily fluctuations of light and temperature, but zones formed only in the new growth. This would seem to eliminate the possibility that zonation in *C. beticola* is due to staling products or aging of the culture.

These data show that zonation is induced by both fluctuating temperature and light. Blue light was comparable to natural diffused daylight, but the red filters apparently cut out the light rays that induced zonation as only traces were evidenced. Ten-minute exposures to light were insufficient to produce zonation which was pronounced under 30-minute exposures. By marking the margins of growth at the time of exposure, it was found that light checks the linear growth of the hyphae, inducing profuse branching to cause the dark bands.

Alternating temperatures produce distinct growth bands (Pl. XXI, Fig. 6); low temperature inhibits growth to such an extent that narrow bands of much-branched, irregular mycelium are produced while wide, light-colored bands are produced from growth at high temperature.

From observations made at various times, medium has had no pronounced influence on zonation, as has neither amount nor depth of nutrients. These, however, are contributing factors in that they affect the expression of growth rings, but in themselves they are not causative factors.

PART II

THE STUDY OF VARIANT FORMS

The attention of the writers was first called to variant forms in *C. beticola* by the occasional occurrence of sectors of differently colored mycelium in colonies of the organism growing on agar plates. At first no particular attention was given to the aberrant sectors until it was observed that they seemed more or less permanent in subsequent transfers if inoculum was carefully selected from the outermost regions of growth so as to take only the aberrant mycelium. These variants always appeared as fan-shaped or wedge-shaped sectors and were noted in practically all the strains under attention. The aberrant form differed from the parental form not only in the color of the submerged mycelium but in the rate of growth of this mycelium. The aërial growth differed also in type, amount, color and density. In the early part of the investigation, only those sectors showing marked differences were selected since they lent themselves more readily to the study. Later, sectors were selected from the various strains under observation which differed less in the color variation. The preliminary transfers of these isolations showed them to be more or less constant, and it seems that the writers are here dealing with a phenomenon similar to that observed and studied by Stevens (1) and Christensen (3, 4) in artificial cultures of *Helminthosporium sativum*, and also by Caldis and Coons (2) in several other species of fungi.

TABLE IX

Temperature in Relation to Zonation in Cultures of *C. beticola*

Agar medium	24° C. Constant				12–24° C. Alternating				12° C. Constant			
	Strain C				Strain C				Strain C			
	1	8	20	27	1	8	20	27	1	8	20	27
Corn meal....	0	0	0	0	+	+	+	+	0	0	0	0
Potato dextrose	0	0	0	0	+	+	+	+	0	0	0	0
Beet leaf......	0	0	0	0	+	+	+	+	0	0	0	0
Oatmeal......	0	0	0	0	+	+	+	+	0	0	0	0
Lima bean....	0	0	0	0	+	+	+	+	0	0	0	0
Malt extract...	0	0	0	0	+	+	+	+	0	0	0	0
Prune juice...	0	0	0	0	+	+	+	+	0	0	0	0
Plain agar....	0	0	0	0	+	+	+	+	0	0	0	0

TABLE X

THE EFFECTS OF TEMPERATURE ON ZONATION IN STRAINS OF *C. beticola*

Strain	Corn meal agar			Oatmeal agar		
	24° C.	24–12° C.	12° C.	24° C.	24–12° C.	12° C.
	Constant	Alternating	Constant	Constant	Alternating	Constant
C–1	0	+ distinct	0	0	+ distinct	0
C–2	0	+ trace	0	0	do.	0
C–3	0	+ distinct	0	0	do.	0
C–4	0	do.	0	0		0
C–5	0	do.	0	0	+ distinct	0
C–6	0	do.	0	0	do.	0
C–7	0	+ very faint	0	0	+ trace	0
C–8	0	+ distinct	0	0	do.	0
C–9	0	do.	0	0	+ distinct	0
C–10	0	do.	0	0	do.	0
C–11	0	do.	0	0		0
C–12	0		0	0	+ trace	0
C–17	0	+ distinct	0	0	+ distinct	0
C–18	0	+ trace	0	0	do.	0
C–19	0	do.	0	0	+ trace	0
C–25	0		0	0	do.	0
C–28	0	+ trace	0	0	+ distinct	0
C–34	0	+ distinct	0	0	do.	0
C–36	0	do.	0	0	do.	0
C–37	0	do.	0	0	do.	0
C–38	0	do.	0	0	do.	0

The aberrant forms were isolated from the parental form by picking a few filaments of the derived fungus from the border of the colony at the center of the sector. If care is taken, pure variant material can be picked out in this way in practically all cases. The variant was then grown on the same plate with the parental form for a number of times in order to test the purity of the material. Out of twenty-odd such selections, in only one does it seem likely that a portion of the normal mycelium was transferred along with the variant and in this particular instance the first planting gave evidence of the mixture. In a few instances spores were produced on the variant forms, in which case single-spore isolations were secured. Morphological studies were made of the variant of strain C–1. Study of the other forms was limited largely to the physiological activities.

The following system was used in keeping the records of the various cultures used in this work. The various strains of *C. beticola* used in this work were labeled C–1, C–2, C–3, etc. Variant forms were labeled v/1, v/2, etc., to indicate the number of times the material had been transferred. The original parental or original material was always grown in parallel cultures on the same plate and labeled as o/1, o/2, etc. Thus (C–1 v/7) refers to the variant form of strain one of *C. beticola* in its seventh transfer and (C–1 o/7) refers to the same strain, but is the normal form which has been grown in parallel culture with the aberrant form.

Occurrence of variant forms. — Of the twenty-three single-spored isolations of the fungus that were studied, fifteen have given rise to one or more variant forms. The occurrence of these aberrant sectors has not been associated with any particular culture medium or other external conditions that can be controlled, since all attempts to induce sectoring have failed. The cultures studied and their derived forms are given briefly as follows:

C–1: Isolated Oct. 31, 1926, from material collected at Rocky Ford, Colorado. Variant forms C–1 v/0; C–1A v/0; C–1B v/0; all white forms and very similar
C–2: Same as C–1. White variant C–2 v/0
C–3: Same as C–1. Variant C–3 v/0. White
C–4: Isolated Oct. 31, 1926, from material collected at Rocky Ford, Colorado
C–5: Same as C–4
C–6: Isolated July 6, 1927, from material received from Oxnard, California. Gave rise to a white variant C–6 v/0
C–7: Isolated Sept. 1, 1927, from material received from Chaska, Minnesota
C–8: Same as C–7. Gave rise to a deep green variant C–8 v/0 and two white variants C–8A v/0 and C–8B v/0
C–9: Isolated Sept. 2, 1927, from material received from Grand Island, Nebraska. Gave rise to three pale green variants with very little aërial mycelium, C–9 v/0; C–9A v/0; C–9B v/0
C–10: Isolated Nov. 5, 1926, from material collected at East Lansing, Michigan. White variant C–10 v/0
C–11: Same as C–10. Variant form C–11 v/0

C–12: Same as C–9

C–13: Same as C–10. A white variant C–13 v/0

C–14: Same as C–9. Variant form C–14 v/0

C–15: Isolated Sept. 4, 1927, from material received from Mason City, Iowa

C–16: Same as C–15

C–17: Same as C–15. Gave rise to two pale yellowish green variants, C–17 v/0 and C–17A v/0

C–18: Isolated Sept. 4, 1927, from material received from Grand Island, Nebraska

C–19: Same as C–18. Gave rise to two pale yellowish green variants which produced a reddish tinge in the substratum, C–19 v/0 and C–19A v/0

C–20: Same as C–18. Gave rise to a pale yellowish green variant form C–20 v/0

C–21 — C–35 inclusive, were Michigan State College Experiment Station stock cultures and were not used extensively, and so will not be listed individually

C–36: Isolated Sept. 8, 1927, from material collected at Rocky Ford, Colorado. Variant form C–36 v/0

C–37: Same as C–36

C–38: Same as C–36

Growth on artificial media. — Cultural histories of the derived forms of cultures C–1, C–8, C–9 and C–19 are given in Plate XXIII typifying the procedure followed in the study of the variant forms. C–1 v/0 is the oldest variant, having been kept through twenty transfers on artificial media for a period of fifteen months. The cultural characteristics of this form on various media are given in Table XI. The aberrant characters can be modified, but not changed by growing the variants on a medium different from that in which it originated. Generally speaking, the aberrant characters become more pronounced with continued culture on artificial medium. C–8 v/0, a variant darker than its parental form, has been an exception. Except for the instances cited under "Apparent Reversions," the derived forms have apparently been constant on artificial media throughout the period of these studies.

Morphological characters of C–1 *and its derived form* C–1 v/0. — Camera lucida drawings of the submerged mycelium from cultures on various media are shown in (Pl. XXI, Figs. 6–9). The mycelium of the aberrant form is characterized by being smaller and less tortuous, and more hyaline with fine granular cytoplasm, with fewer of the large translucent oil globules indicating a different

TABLE XI

GROWTH OF *C. beticola* VARIANT FORM C–1 v/0 AND ITS PARENTAL FORM C–1

Agar medium	Parental			Variant		
	Diam. mm.	Submerged	Aërial	Diam. mm.	Submerged	Aërial
Plain	23	Pale green	Slight, gray	27	Colorless	None
Prune juice	24	Olive green	Abundant, gray felty	36	do.	Sparse, tufted
Litmus lactose	19	Dark green	Low, felty, grayish-green	24	do.	Low, wet, felty
Beet leaf	19	Greenish-black	Short, dark, mealy conidia	22	do.	None
Malt extract	24	Greenish-gray	Abundant, felty, gray	28	do.	Abundant, low
Neutral red	9	Black	Tufted, grayish-black	13	do.	Tufted
Endo's	16	Green	Short, deep greenish-gray	20	do.	Sparse
Lima bean	24	Greenish-black	Abundant, light gray, felty	23	do.	Sparse, wet, felty
Bean pod	25	Greenish-black	Abundant, gray-green, felty	27	do.	Sparse
Oatmeal	21	Light green	Sparse, greenish-gray	24	do.	Sparse
Potato dextrose	12	Olive green	Abundant, greenish-gray	20	do.	Sparse
Corn meal	25	Olive green	Greenish-gray	28	do.	Sparse

food storage capacity than the parental form. The loose sclerotium-like bodies so often found in the submerged mycelium of the normal form have never been observed in this aberrant form.

As previously stated, the length of conidia and the number of septa per conidium in *C. beticola* are variable factors depending somewhat upon nutrients, humidity and temperature. The variant form of strain C–1 has been practically sterile throughout its cultural history, but a few very small conidia were produced on C–1 v/7 growing on beet leaf agar. Measurements were made of twenty conidia picked at random from washings of the culture and compared with a like number from C–1 o/7.

TABLE XII

A Comparison of Conidia Produced by the Variant C–1 v/7 and Its Parental Form C–1 o/7

Form	No. of septa			Length in mm.			Width in mm.
	Max.	Av.	Min.	Max.	Av.	Min.	
C–1 o/7	22	10.8	4	260	138	55	4–5
C–1 v/7	6	4.6	2	52	35	24	3.2–4.3

The data given indicate that the differences in average size of conidia and the number of septa per conidium between the parent and variant forms are very great. The spores produced by the variant form are more hyaline with more finely granulated cytoplasm than those from the normal form. No difference could be noticed in germination of the conidia in hanging drops of distilled water and nutrient broth. Subcultures arising from single conidia obtained from the variant culture gave colonies indistinguishable from the variant.

Passage through plants. — Inoculation of sugar beets with form C–1 v/0 was tried several times without success, but on two occasions a few small brown flecklike spots were produced. Conidia were not produced on the plant, so re-isolations were made from mycelium at the border of the spots. C–8A v/0, another white form, showed very little attenuation in that infection was easily effected, and conidia were produced in the older spots. Both these forms on re-isolation were pale green and had regained to some extent the power to produce aërial mycelium. Microscopic examination of the submerged mycelium of C–1 v/0 on corn meal agar showed it to be quite similar to its parental form C–1. The pale yellowish-green variants produced infection as readily as did their parental forms and on re-isolation were practically the same in color. However, the tendency to produce sparse aërial mycelium was still evident but somewhat overcome. Variant form C–8 v/0 seemed to be more virulent than its parental form, but on re-isolation in artificial culture was hardly distinguishable from it.

These inoculation experiments brought out three important facts: first, that there is at least a tendency for restoration to the normal form; second, that the greater the variation the greater the change toward the normal; and, third, that the origin of these aberrant forms is possibly due to malnutrition, since the sugar beet is the natural medium for its growth.

ATTEMPTS TO PRODUCE VARIANTS

As detailed by Brierley (1), various workers have produced "mutations" in *Aspergillus niger* and *Penicillium glaucum* by treating the cultures with various chemicals. Brierley (1) has tried to repeat this work, using strains of the same fungi, without success. Stevens (11) reports unsuccessful attempts to produce "saltations" in *Helminthosporium sativum* by wounding and various other methods. The senior writer has carried out the following outlined attempts to produce aberrant forms in normal cultures of *C. beticola.*

Wounding. — The tips of actively growing hyphae in cultures C–1 and C–27 growing on corn meal agar were killed by means of a hot platinum wire in several places around the border of the colony. The injured areas soon outgrew the injury; the margins of the colonies presented a uniform appearance. These results are strengthened by the fact that variations have never been found to arise in cultures at the point from which inoculum has been procured with a hot needle.

Illuminating gas. — Since gas poisoning of cultures is always a possibility under laboratory conditions, the writers sought to determine whether this factor was responsible for sector formation in normal cultures. Two-week-old cultures C–1 and C–27 were placed in a series of air-tight chambers and treated with illuminating gas for periods of 4, 6, 8, 10 and 24 hours. The gas was allowed to pass through the chamber for thirty minutes, thus forcing out all the air. Cultures exposed to 4- and 6-hour treatments were only slightly inhibited in growth as compared with the checks. Eight- and 10-hour treatments inhibited growth completely but did not kill the organism, since inoculum put on corn meal agar produced normal growth, while 24-hour treatment killed the fungus. The cultures were kept in the laboratory for three weeks after treatment without any sign of variation, nor have any of the subsequent transfers given rise to aberrant forms.

Freezing. — Many of the aberrant forms under observation have appeared during the winter months, so cultures of the organism were frozen with carbon dioxide gas in an attempt to induce formation of variant sectors by exposure to extremely low temperatures. The methods of freezing were varied, one to thirty minutes continuous freezing being applied to some cultures, and others were alternately frozen and thawed for different lengths of time. The treated cultures were allowed to grow for ten days and then subcultures were made from the frozen areas, but none of the treated cultures or the subsequent transfers gave any indications of throwing variants.

Poisoning with chemicals. — In an attempt to induce the throwing of variants, vigorously growing cultures of the fungus were treated with chemicals chosen because they were strong oxidizing or reducing agents. Small crystals of $K_2Cr_2O_7$ and drops of solutions of KNO_3, H_2O_2 and CHOH were placed at different points around the margins of the colonies. In this manner different concentrations were obtained as diffusion of the chemicals through the medium took place outwardly from the points of application. The fungus was killed at the points of application, and growth was inhibited to a variable degree, depending upon the concentration of the chemicals, but subsequent growth was normal, with no indication of variants. Subcultures made from different portions of the treated colonies gave only normal forms.

These attempts and others of a similar nature have been tried at various times by the second writer, but always with negative results. They indicate that the coarse methods used were not so directed as to upset the equilibrium within the fungus cells, rather than exhausting the possibilities of success through methods of this sort.

MECHANICS OF SECTOR FORMATION

Artificial sectors were produced by both mixed planting and implanting of two forms in an attempt to show the mechanism of sector formation. Stevens (11) used these methods in an attempt to demonstrate that ordinary transfers might be mixtures of two forms or races, thus explaining the appearance of "saltations." He obtained no segregation of forms in mixed plantings and only partial success by implantings.

Implantings of mycelium from an achromatic form at the border of a normal green culture gave rise to typical sectors only when the implanted material had a chance to start active growth before the advancing mycelium of the normal form engulfed it, in which case the planting was obscured. If the implanted material starts growth, a typical wedge-shaped sector is formed. There seems to be very little antagonistic influence between forms of *C. beticola,* since two forms will grow parallel with each other, but with very little intermingling of hyphae. The forms can be isolated in pure culture from the borders of the colony.

Mixed plantings. — Acting upon the knowledge that the variants were frequently more rapid growers than the parental form, the writer made mixed plantings to determine whether or not the two forms would segregate and remain distinct. Equal amounts (one square centimeter) of agar and its contained mycelium from each form were thoroughly mixed under aseptic conditions, and the mixture used as inoculum on corn meal agar plates. Several forms have been treated in this manner, but strain C–1 and its variant, and strain C–8 and its variant, have shown the best contrast. Segregations took place in the form of several wedge-shaped sectors resembling the normal and the aberrant sector from which the forms were obtained (Pl. XXII).

The results of this experiment seem very important in explaining what happens in naturally developing sectors. If in a culture two elements of different potentialities develop, then if the growth rates are approximately the same or if one is only slightly greater than the other, there will be produced sectors of the one form in the other. The results from mixing the mycelium together would indicate that a small amount is sufficient to inaugurate a sector; perhaps only a single cell would be sufficient if not repressed by the surrounding growth.

APPARENT REVERSIONS

Several instances of apparent reversion of the aberrant characteristics have been observed. Such reversions always occurred as normal sectors in the aberrant form, and these sections have differed from the variant in colony color, amount and density of the aërial mycelium and in spore production. Achromatic sectors have appeared on beet leaf agar that immediately reverted *en masse* to the normal form, but these variants have not been considered stable. Only reversions of the stable forms through sectors are here considered.

Reversion has been found to be most common in forms just isolated from the aberrant sector. Aberrant form C-13 v/0 has shown a great tendency to split up into normal and variant forms (Pl. XXI, Fig. 3 B). Continued selection for the contrasting types has finally resulted in an achromatic variant C–13 v/7 that has been stable through the last three transfers. Variant form C–20 v/3 developed a normal sector in a five-day culture that was identical with the parental form in every respect through two subsequent transfers, and the variant form has shown no further tendency to split into the two forms. Variant forms C–6 v/1, C–14 v/2 and C–27 v/1 all showed tendencies toward reverting to the parental form, but selections for the aberrant characteristics have resulted in phenotypic cultures.

The producton in these variant forms of the duplicate of the parental forms, under conditions in which it seems that mixture of the parental material was excluded, seems very significant.

DISCUSSION

The development of variations in the mycelium of *C. beticola* has been noticed throughout the two years of study of the various strains. These variants have appeared as wedge-shaped sectors in normal cultures, being most noticeable for their lack of color, sparse aërial mycelium and sterility on beet leaf agar. Some of these have reverted more or less to the normal form in color, but the mycelial characters have remained constant; intensity of color only is influenced by the medium on which the organism is growing. Some of the aberrant forms, C–1 v/0 in particular, have been remarkably permanent on artificial media. Passage through plants has a tendency to intensify the color of the mycelium. Variant forms C–1 v/0 and C–8 v/0 were pure white when growing on artificial media, but became almost normal green after passage through sugar beets. The density and amount of aërial mycelium and type of growth in the substratum were influenced to some extent by passage of the aberrant forms through the host plant.

There has been developed an extensive literature on variations occurring in pure cultures of asexual fungi. Brierley (1) and Stevens (11) have compiled complete bibliographies on the subject, from which material has been extensively used. Contradictory views regarding the nature of these variant forms have been expressed by various investigators. The bulk of the literature, however, merely reports the occurrence of such variations along with certain morphological characteristics and physiological reactions, without dealing extensively with the genetic nature of the variations. One group of investigators believes these variant forms to be true "mutations" or "saltations" comparable to the so-called bud mutations which occur in apparently pure line cultures of plants, of which view Stevens (11) and Christensen (4) are the strongest exponents. Opposed to this view are those who believe, with Caldis and Coons (2), that they are modified forms of a more or less permanent nature. They have based their belief upon the assumption that if a change in the genetic constitution of the organism, as Brierley (1) has defined a mutation, had actually taken place, the very common occurrence of reversion to the normal form would not then be likely.

Whether or not the variations studied and recorded in this paper are "mutations" or "saltations," or are merely modified forms, it has been found that they are only semipermanent in certain of these characters. The actual cause of their development remains as yet unknown, but the changes are of such a type as to suggest nutritional disturbances as playing an important rôle. The sparse aërial mycelium can also possibly be explained as a result of attenuation of the organism through malnutrition.

In the absence of exact knowedge of the life-history of the organism other than the asexual stage, conclusions concerning the actual nature of the variant forms cannot be drawn, but at least it can be said that the claim that these variants represent "mutations" is at all events far from being proved.

SUMMARY

C. beticola is the fungus causing Cercospora leaf-spot of sugar beets.

The organism was found to grow well on most standard culture media. Light apparently plays a minor rôle in its development; temperature materially affects the vegetative growth.

Conidial production in artificial cultures was found to be a response to a nutrient stimulus, light and temperature influences being flexible.

Zonation in artificial cultures is due to the differential growth of mycelium and not to conidial production. It has been induced by fluctuating light and temperature conditions. Other factors influence, but do not initiate, zone formation.

Variant forms appearing as wedge-shaped sectors were isolated from known single-spore cultures of *C. beticola*. These aberrant forms have been constant on artificial media. Passage of the aberrant forms through sugar beets has had a tendency to restore the normal color, but has only partially affected some morphological characteristics.

Attempts to produce variants by wounding, exposure to illuminating gas and low temperatures and by treating with chemicals have been unsuccessful. By mixing normal mycelium with a variant culture the subsequent growth showed sectoring simulating the normally occurring type, thus indicating the mechanics of sector formation.

The behavior of these variant forms indicates that they may be looked upon as modified forms with nutritional disturbances playing a rôle in their development.

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EXPLANATION OF PLATES XXI–XXIII

PLATE XXI

Fig. 1. Multi-septate conidiophores and conidia produced on plants growing under humid conditions in the greenhouse

Fig. 2. Abnormal hypha-like aged conidiophores of *C. beticola* growing in pure culture

Fig. 3. Newly formed conidiophores of *C. beticola* sporulating in pure culture

Fig. 4. Abnormal conidia, produced in pure culture, showing germ tubes

Fig. 5. Normal germinating conidium from a pure culture

Fig. 6. Normal conidia taken from the host plant

Fig. 7. A, submerged mycelium of the variant form 1 v/9 growing on corn meal agar; B, submerged mycelium of the normal form 1 o/9 on corn meal agar

Fig. 8. Same as Figure 7, except that the fungus is growing on potato dextrose agar

Fig. 9. The two forms growing on beet leaf decoction agar

PLATE XXII

Fig. 1. An abnormally dark sector in a culture of C–8 showing the origin of variant form C–8 v/0

Fig. 2. Cultures showing sectoring produced by mixed plantings of the normal and the aberrant white forms of C–8

Fig. 3. A, the normal culture C–13, and B, its variant form showing reversions to the normal; C, the normal culture C–1 and its variant form after being in culture through eighteen transfers

Fig. 4. A normal sector produced in an aberrant white culture form of C–8 by implanting the normal fungus

Fig. 5. A, cultures showing zonation induced by alternating temperatures; B, transfers of the same cultures kept at constant temperatures

PLATE XXIII

Fig. 1. Diagram showing the cultural history of culture C–8 and its variant forms

Fig. 2. Diagrammatic history of culture C–19 and its variant forms

Fig. 3. Cultural history of C–1 and its variant form C v/0

Fig. 4. Cultural history of C–9 and its variant forms

PLATE XXI

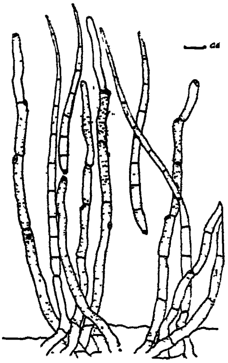


FIG. 1

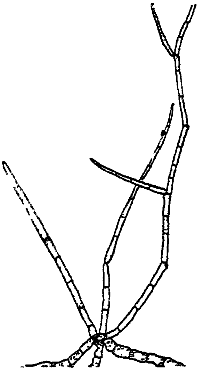


FIG. 2

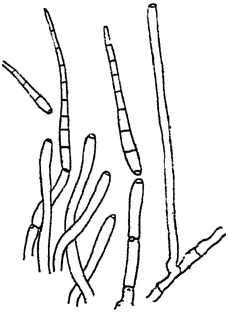


FIG. 3

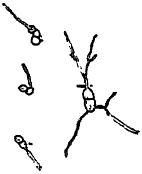
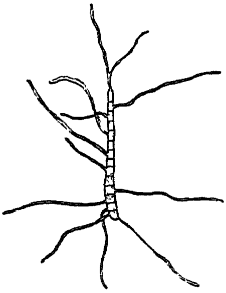


FIG. 4



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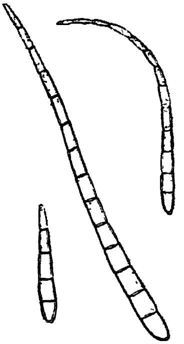


FIG. 6

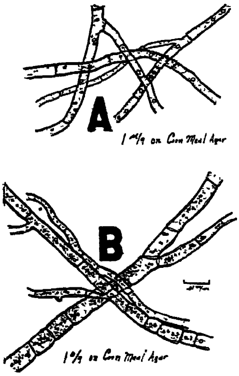


FIG. 7

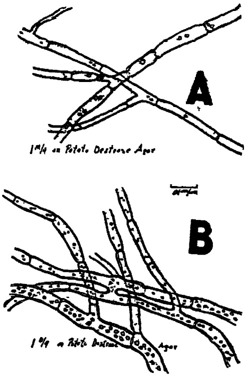


FIG. 8

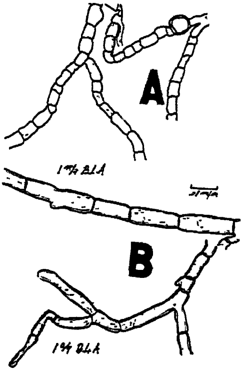


FIG. 9

PLATE XXII

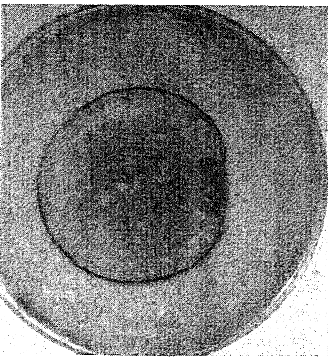


FIG. 1

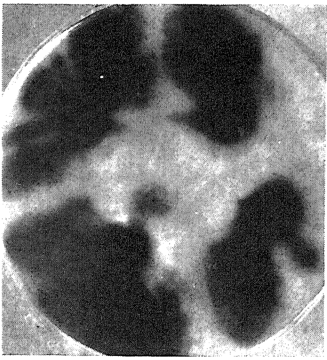
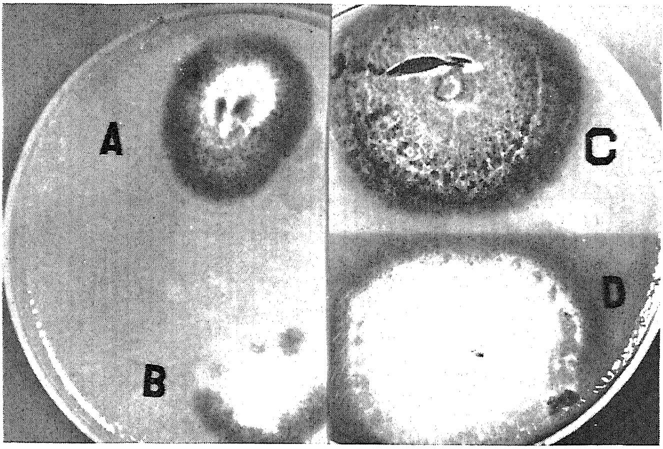


FIG. 2



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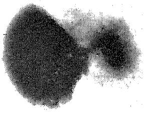

FIG. 4

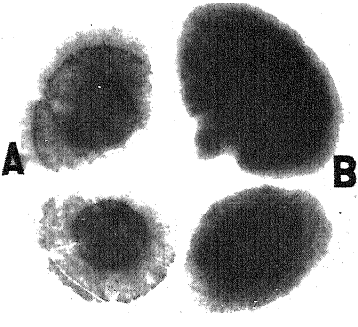

FIG. 5

PLATE XXIII

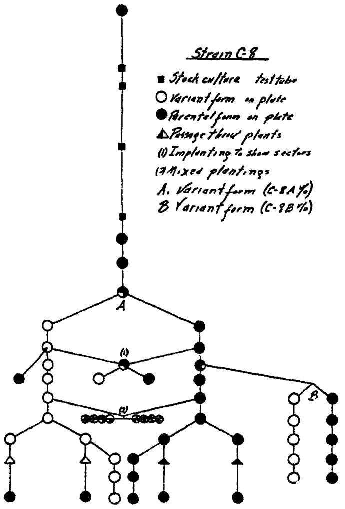

Fig. 1

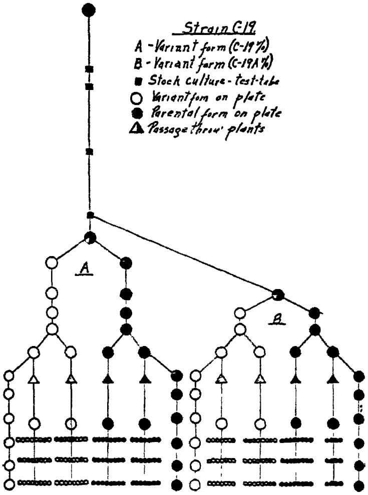

Fig. 2

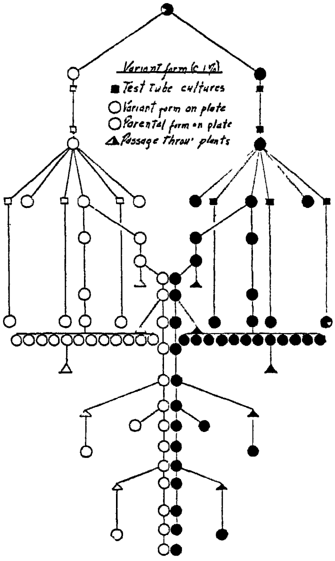

Fig. 3

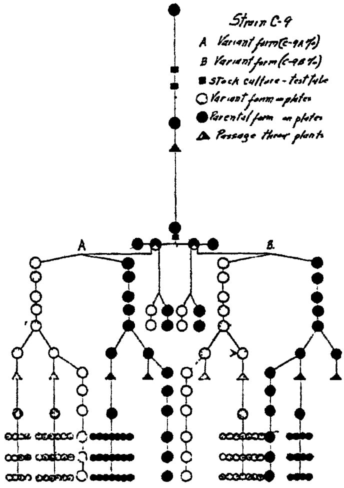

Fig. 4

MONTANA DISCOMYCETES FROM THE FLATHEAD NATIONAL FOREST *

GEORGE B. CUMMINS

THE Discomycetes here reported on were collected in the course of an expedition to the Flathead country of Montana, for the purpose of collecting its flora, phanerogams as well as cryptogams. The material is deposited in the Herbarium of the University of Michigan. The party consisted of Dr. C. H. Kauffman, director of the Herbarium, and Mr. Cummins, as his assistant.

We are under deep obligation to Mr. Lloyd Hornby, supervisor of the Flathead National Forest, for his generous help and many courtesies. He provided us with a cabin, bedding, horses and other conveniences and arranged for our meals at the Ranger Station where the cabin was. Mr. J. E. Thompson, the experienced ranger of the Echo Lake Station, not only showed us how a first-class Ranger Station should be run, but helped us in many ways to be comfortable and to accomplish our ends. To both of these men we are truly grateful. The Director is especially indebted to the Dean of the Graduate School and to the Graduate Board of the University of Michigan for an allocation from the Graduate research fund, to help defray the expenses of himself and his assistant on this expedition.

During the period from June 26 to August 2, 1928, it was the writer's privilege to botanize in a portion of the Flathead National Forest, a region rich in plants and as yet little explored. The location selected was the Echo Lake Ranger Station, thirty miles from Kalispell, at the base of the Swan Range. The mountains at this point rise rather abruptly from a gently sloping, swampy,

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* Paper from the Department of Botany of the University of Michigan No. 308, and from the University Herbarium, No. 12.

forested region giving considerable variation in topography and elevation without necessitating an undue amount of travel. The elevation varied from 3000 feet to approximately 7000 feet at the summit of the range. Numerous canyons afforded a variety of exposures and soil types varying from a heavy forest humus to light gravelly soil. The lower flats presented nearly all conditions of swamp soils. Along with some general collecting, the writer gradually began to try to obtain as many Discomycetes as possible during the latter part of the period. This was done mostly in the forested region of the flats at the base of the mountains.

The forest at the base of the mountains consisted mainly of a dense, highly overmature stand of fir, spruce and pine, with the usual willow and poplar types along the streams and the lower swampy ground. On the higher elevations it graded off into alpine fir. White cedar was present in restricted stands.

Streams were numerous and spread out or disappeared on the flats at the base of the range. In addition to this rather constant moisture supply the rainfall was unusually heavy for this region, making conditions favorable for a variety of collecting.

Discomycetes, as compared with fungi in general, were most favored by the special type of prevailing moisture conditions, as well as by the abundance of decaying organic matter. It seems to be a characteristic of the fruiting of Discomycetes that the moisture requirements are different from those of many other fungi, especially the Basidiomycetes. Alternating wet and dry periods, of short duration, appear to be much more favorable to their normal development than are the steady rains and low hanging fogs which favor most the appearance of agarics. Some interval of dry weather, following a rain, is more propitious. Such rains interspersed with warm dry weather featured the July period at Echo Lake. As a result, a good representative collection of the early summer species was obtained.

After leaving Echo Lake in early August, we collected a few species in Bitter Root Forest, near Darby, Montana. Moisture conditions were far less favorable here, but otherwise the country is very similar to that around Echo Lake. So far as was possible, identifications were all made at the Ranger Station by the use of several standard works which we had with us. In this way their study was always done with fresh material.

Few reports concerning the fungus flora of Montana have appeared. Graff (1–2) has begun to publish a series of lists, but as yet has not included the Ascomycetes. No special account of the Discomycetes has come to the writer's attention; the occasional species reported were from material sent to the various students of the group. Zeller (13–14) has reported several species of Discomycetes from Oregon. Sydow and Petrak (12) and Rehm (5–9) report or describe scattered species from northwestern United States. Studies of the fungus flora of the Southern Rockies have been more thorough (see Seaver, 10; Kauffman, 3).

Identifications were generally made with the use of Rehm's Discomycetes (4). Such as were included by Seaver in his *North American Cup-Fungi* were later verified or changed. The general arrangement of families follows that given by Engler and Prantl; the genera used are in the sense of Rehm. The species were collected and identified largely by the writer and every care was exercised, with the means available, to insure the accuracy of their identification.

In this list species collected in Bitter Root Forest, near Darby, Montana, are indicated by an asterisk (*).

HELVELLALES

GEOGLOSSACEAE

MITRULA PHALLOIDES (Bull.) Chev.* — Common on submerged spruce needles in wet bogs. Darby.

HELVELLACEAE

HELVELLA ALBIPES Fkl. — The plants in this collection are smaller than is characteristic for this species. The white, subpubescent stem, brownish hymenium, and the spores (18–23 × 12–15 μ) make it quite certain, however, that it is only a minor form of *H. albipes*. On soil and very rotten wood. One collection. Echo Lake.

HELVELLA ATRA König. — On soil and wet rotten wood. One collection. Echo Lake.

HELVELLA CRISPA (Scop.) Fr. — Only one specimen, very immature, was found. On soil in woods. Echo Lake.

HELVELLA ELASTICA Bull. — On soil. One collection. Echo Lake.

HELVELLA INFULA Schäff. — Apparently common but scattered. On soil. Echo Lake.

HELVELLA SPHAEROSPORA Pk. — Only one specimen of this rare fungus was found, but it was fully developed and in excellent condition. The spores average 9–11 μ. The paraphyses are enlarged at the light brown tips to a diameter of 9–12 μ.

RHIZINACEAE

PSILOPEZIA AQUATICA (DC.) Rehm. — This was a very pallid form which darkened to orange on drying. On wood continually wet by spray. One collection. Echo Lake.

"PSILOPEZIA ORBICULARIS (Pk.) Dodge." — According to Seaver, this is *Peziza clypeata* Schw. On rotten wood. Common. Echo Lake.

PSILOPEZIA NUMMULARIA Berk. — On rotten wood. One collection. Echo Lake.

PEZIZALES

PYRONEMACEAE

PYRONEMA DOMESTICUM (Sow.) Sacc. — The spores of the plants in this collection are too large to allow of its being placed in *P. omphalodes* (Bull.) Fkl. They measure 14–18 × 9–11 μ. On burned-over ground and on charcoal. One collection. Echo Lake.

PEZIZACEAE

ACETABULA SULCATA (Pers.) Fkl. — Common along streams and in wet moss. Abortive forms also occur in the water and resemble *Ombrophila Clavus* (A. & S.) Cooke more than they do *A. sulcata*. Common. Echo Lake.

DISCINA ABIETINA (Pers.) Rehm. — On mossy ground. Only two poorly developed plants were found. Echo Lake.

Geopyxis cupularis (L.) Sacc. — On the ground in woods. Common. Echo Lake.

Humaria coccinea (Crouan) Quél. — In its younger stages this species was often half submerged in the soil. Other characters exclude it from *H. semiimmersa* (Karst) Sacc., however. The apothecia reach a diameter of 5 mm., but average about 3 mm. The margin is wavy to nearly fimbriate and thin; the base of the cup is relatively thick. Spores 30–38 × 9–12 μ. On soil. One collection. Echo Lake.

Humaria Gerardi (Cooke) Sacc. — On soil full of rotten wood. One collection. Echo Lake.

Humaria leucoloma (Hedw.) Boud. — The spores of these plants measured 16–20 × 8–11 μ, which is slightly smaller than the size given by Seaver. On mossy ground. One collection. Echo Lake.

Lachnea Erinaceus (Schw.) Sacc. — Common on rotten wood and débris. Echo Lake.

Lachnea flavo-brunnea Rich. — The apothecia reach a diameter of 1 cm., are sparsely beset with brown hairs, and only rarely flatten out entirely. The hymenium is pallid to light ochraceous, darkening but little on drying. Asci cylindrical, 135–175 × 8–11 μ; 8-spored in one series. The spores are smooth, hyaline, elliptical, with two small oil drops, 12–15 × 6–8 μ. On coniferous wood and débris. One collection. Echo Lake.

Lachnea hemisphaerica (Wigg.) Gill. — On very rotten wood. Common. Echo Lake.

Lachnea setosa (Nees) Gill. — The hymenium of the plants in our collection is deep chrome (Ridg.), rather than deep red, probably owing to the moisture conditions under which they grew. In all other respects the plants are typical. On wood continually wet by spray. One collection. Echo Lake.

Lachnea scutellata (L.) Gill. — On wood. Common. Echo Lake.

Lachnea umbrorum (Fr.) Gill. — On wet sandy soil. Common. Echo Lake.

LAMPROSPORA CONSTELLATIO (Berk. and Br.) Seaver. — On wet soil and leaf mold. Common. Echo Lake.

MACROPODIA CORIUM (Weberb.) Sacc. — On moist clay soil in deep woods. One collection. Echo Lake.

MACROPODIA MACROPUS (Pers.) Fkl. — On very rotten wood and débris. Common. Echo Lake.

OTIDIA AURICULA (Schäff.) Rehm. — On sandy soil and in moss along streams. Frequent in restricted areas along Birch Creek. Echo Lake.

PLICARIA BADIA (Pers.) Fkl. — On soil and rotten wood. Common. Echo Lake.

PLICARIA BRUNNEO-ATRA (Desm.) Rehm.* — On soil and very rotten wood. Two collections. Echo Lake and Darby.

PLICARIA REPANDA (Wahlb.) Rehm. — On wet rotten wood. Common. Echo Lake.

PLICARIA VIOLACEA (Pers.) Fkl. — On decaying moss in a boggy meadow. One collection. Echo Lake.

PSEUDOLPLECTANIA NIGRELLA (Pers.) Fkl. — On swamp humus. One collection. Echo Lake.

ASCOBOLACEAE

ASCOBOLUS FURFURACEUS Pers. — On deer dung. One collection. Echo Lake.

LASIOBOLUS EQUINUS (Müll.) Karst. — On deer dung. Common. Echo Lake.

HELOTIACEAE

DASYSCYPHA ACUUM (A. and S.) Sacc. — This is a very minute species appearing as white points scarcely visible without the aid of a lens. On needles of fir and spruce. One collection. Echo Lake.

DASYSCYPHA DRYINA (Karst.) Sacc. — No spores were obtained, but other characters make it seem probable that this is the the correct placing. One collection. Echo Lake.

GORGONICEPS GUERNISACI (Crouan) Sacc.* — The plants in our collections rarely exceed a diameter of 1 mm. On drying the hymenium becomes nearly black, but with moistening it readily regains the characteristic grayish-yellow color. Without exception the plants were found on wood which was continually wet with spray or which was completely submerged, often in very rapidly flowing water. On wood of willow and alder. Common. Echo Lake and Darby.

HELOTIUM CITRINUM (Hedw.) Fr. — On wood of deciduous trees. Common. Echo Lake.

HELOTIUM EPIPHYLLUM (Pers.) Fr. — On leaf remains and decaying fir cone. One collection. Echo Lake.

HELOTIUM HERBARUM (Pers.) Fr. — On herbaceous stems. One collection. Echo Lake.

HELOTIUM SORDIDATUM Karst. & Starb. — On decayed leaves of birch and alder. Common. Echo Lake.

LACHNELLA CORTICALIS (Pers.) Fr. — On wet decorticated log. One collection. Echo Lake.

LACHNUM BICOLOR (Bull.) Karst. — On dead stalks of *Rubus parviflorus* Nutt. and on other small twigs. One collection. Echo Lake.

LACHNUM NIVEUM (Hedw.) Karst. — On dead stalks of *Rubus parviflorus* Nutt. and occasionally on stalks of rose. Common. Echo Lake.

LACHNUM SPIREAECOLUM (Karst.) Rehm. — The stems of the plants of this collection varied between 1 and 4 mm. in length, but in other respects they agreed with Rehm's description and remarks. The cup is not densely haired and seldom becomes entirely expanded. On exposed dead roots and dead stems of some shrub. One collection. Echo Lake.

PEZIZELLA ALBO-PUNCTA (Pk.) Sacc. — Apothecia subsessile, minute, 0.1–0.3 mm., white when fresh, but drying light yellow. The asci have very heavy walls, especially at the pores, and become abruptly narrowed to a short stalk below the spore-bearing portion; 60–90 × 9–13 μ, 8-spored. Spores obliquely uniseriate or biseriate in the ascus at maturity. The spores are elliptical, one-celled, hyaline, smooth, straight or slightly plano-convex, and usually contain two oil drops; 12–18 × 4–6 μ. Paraphyses filiform or slightly enlarged upward; 2–4 μ. On leaves of Cornus (?). One collection. Echo Lake.

PEZIZELLA CONORUM Rehm. —The spores of the plants in our collection were immature, but in all other respects they agree with Rehm's description of this species. On decaying cones of fir and spruce. One collection. Echo Lake.

BULGARIACEAE

OMBROPHILA CLAVUS (A. & S.) Cooke.* — This species has been the subject of considerable discussion. Rehm gives descriptions of both *O. Clavus* and *Ciboria uliginosa* (Fr.) Rehm, but later reduced *C. uliginosa* to synonymy. Von Höhnel, in his *Fragmente zur Mycologie* (1918), includes *O. Clavus* in his discussion of the genus Ombrophila. He says: "Diese Art ist durchaus nicht gallertartig. Ihre Untersuchung zeigte mir, dass sie im wesentlichen parallelfaserig aufgebaut ist, jedoch nicht so rein und streng wie *Phialea.*" The plants in our collection have a slight peridial layer which is perhaps not truly gelatinous, but the remainder of the cup is certainly sufficiently so, thus indicating an Ombrophila rather than a Ciboria.

They were always found on wood in water or in drifts which were continually wet with spray. Many were found on sticks completely submerged in rapidly flowing water. Common. Echo Lake and Darby.

OMBROPHILA VIOLACEA (Hedw.) Fr. — On wet rotten wood. One collection. Echo Lake.

ORBILIA LEUCOSTIGMA Fr. — On rotten wood. One collection. Echo Lake.

MOLLISIACEAE

MOLLISIA CAESIA (Fkl.) Sacc.—On dead willow sticks. Common. Echo Lake.

MOLLISIA CINEREA (Batsch) Karst. — On wood. Common. Echo Lake.

NIPTERA CITRINELLA Rehm. — On dead alder branch. One collection. Echo Lake.

NIPTERA RAMINCOLA Rehm.* — Superficially this plant appears to be *Mollisia cinerea,* but examination shows the spores to be 1–3-septate. On old wood in wet drift piles. Common. Darby.

PATELLARIACEAE

PLEIOPATELLA HARPERI Rehm. — Our plants agree with Rehm's description very well. The fact that the ascus contains one large, hyaline, muriform spore makes it a very distinctive plant. Algal cells seem to be present in the base of the apothecia and the first inclination was to place it under the lichen species, *Biatorella moriformis* (Ach.) Th., on the assumption that it might represent an immature condition of a plurispored ascus. Since it is certainly the species treated by Rehm and since no authentic material of *B. moriformis* is at hand to serve as a comparison, it is refered to the genus Pleiopatella. On the bark of standing trees of white cedar. Echo Lake.

PHACIDIALES

PHACIDIACEAE

Pseudographis tetraspora, sp. nov. — APOTHECIA not intergrown with the substratum, at first submerged, later breaking through and becoming nearly superficial, broadly hysteriform, black, leathery when fresh to horny and tough when dry, reaching 3 × 1 mm.; peridium dark brown to black. HYMENIUM whitish; epithecium dark brown. ASCI cylindrical to clavate, 175–225 × 15–18 μ, 4-spored in two series, not stained blue with iodine. SPORES cylindrical with obtuse rounded ends, tinted greenish with a wide hyaline border, smooth, slightly curved, 6–10-celled, 75–95 × 8–10 μ. PARAPHYSES filiform, septate, tips brownish, twisted, forming an epithecium. (See Fig. 1.)

On decorticated wood of *Thuja occidentalis* Nutt. Type collected by George B. Cummins, July 30, 1928, near Echo Lake, Montana.

This is a very characteristic species. The large spores and the 4-spored condition of the asci make it distinct from the other described species of this genus. Rarely the asci may contain only two spores. The spores tend to break into fragments in mounting for study, but it is not constant enough to be considered a character. The hyaline border of the spore swells in water, but gives no sign of dissolving.

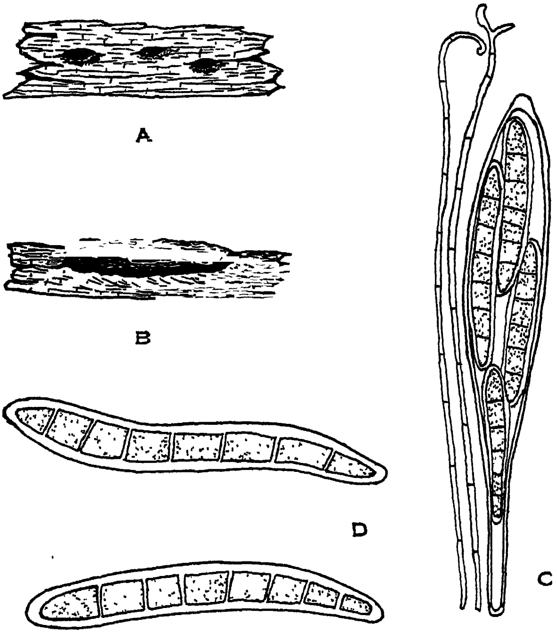

FIG. 1. PSEUDOGRAPHIS TETRASPORA Cumm., sp. nov. *a*, habit sketch showing apothecia; *b*, apothecium enlarged to show broad opening and membranous margin; *c*, typical 4-spored ascus and paraphyses; *d*, ascospores showing the hyaline border

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FIELD OBSERVATIONS ON WILD ROSES OF THE WESTERN UNITED STATES*

EILEEN WHITEHEAD ERLANSON

THE writer made a trip in the autumn of 1928 for the purpose of studying and collecting seeds of western wild roses. Stations were visited in Utah, Nevada, Oregon, California and New Mexico.

PARALLEL VARIATION OR HYBRID SWARMS?

The most striking general phenomenon in any large series of wild roses is the occurrence of certain minor characteristics in each of the larger species groups or collective species, and their combination in almost every possible manner. This fact has been observed in other genera (Vavilov, 12; Hall, 5) and has led to attempts at tabulation of the total possible number of rose "species."

The characteristics in question are for the most part those that Hurst (6) classes as "varietal and formal characters." Field observations confirm this view. It is probable that these variations are Mendelian in behavior and, if they occur in every interbreeding population, they are obviously of little use for distinguishing species. They are concerned chiefly with the prickles, indument of leaflets, teeth, hip form and sepals, and are listed below:

Prickles, straight; curved or deflexed; absent
Leaflets, thin, firm; glabrous, pubescent, glandular-puberulent
Teeth, simple and eglandular; serrulate and gland-tipped
Hips, pyriform, ampulliform or urceolate; globose, depressed-globose
Sepals, smooth, glandular-hispid

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These characteristics were observed in:

(*a*) The group of *Rosa Woodsii* (diploid), in Utah and Nevada.
(*b*) The group of *Rosa pisocarpa* (diploid), in northern California and Oregon.
(*c*) The group of *Rosa californica* (tetraploid), in California.
(*d*) The group of *Rosa nutkana* (hexaploid), in northern California and Oregon.
(*e*) In *Rosa gymnocarpa* (diploid), in California and Oregon.

It has been customary in the past to describe the plants in each group showing different combinations of these characteristics as species. This leads to artificial classification, owing to the trivial nature of the characteristics often used to separate whole groups of species in an analytical key (Rydberg, 9). In *R. gymnocarpa* even Dr. Rydberg (8) admits that Greene's species founded on these variations are (with the exception of the pubescent *R. Bridgesii*) only "tentative species" or "fairly good varieties," and that many "are hardly worth naming as forms." The more the writer studies the other North American collective species in the field and garden, the more convincing it becomes that the species in other groups, based on such variations, are no more reliable than those in the Gymnocarpae.

The frequency with which these variants occur within each species and in different geographical areas is important, but this could be expressed more clearly if they were represented in tabular form under the main species. The method suggested by Vavilov (12) might be followed in Rosa; that is, each minor characteristic could be designated by a letter, then the various combinations expressed as a formula, thus obviating the necessity for multiplying indefinitely the specific or varietal names. Vavilov proposes this method for designating parallel variations, but Babcock and Clausen (1) have pointed out that the term "parallel variation" "should be confined to the independent origin of parallel series of variations in distinct species," and not to Mendelian recombinations. The roses of North America seem to be of the kind of groups that Cockayne (3) calls "hybrid swarms," and as yet nothing is known of the parts played by hybridization and mutation in the production of the variations. I have reported the occurrence of many combinations of "specific characteristics" within the progeny of one plant of *R. blanda* var. *glandulosa* (Erlanson, 4).

Scattered plants of the western roses were observed bearing many aborted hypanthia together with few, and sometimes no, normal hips. These often grew among plants bearing numerous plump hips. Such plants were seen in all the major species, with the exception of *R. gymnocarpa.* This observation agrees with the discovery of a large percentage of sterile pollen among native wild roses, a phenomenon generally thought to be indicative of a hybrid condition.

THE DIPLOID ROSES

Cytological studies have shown that the majority of the western Cinnamomeae are diploid with fourteen somatic chromosomes.

These species are widespread in the region visited, being characteristic of stream banks, ditches and lake shores. In the artemisia-piñon regions of the Great Basin, roses of the *R. Woodsii* Lindl. affinity are to be found wherever there is a little seepage or enough water to support willows. The summer of 1928 was an unusually dry season and a small stream near Virginia City, Nevada, had dried up completely. Large willows and roses growing beside it were shriveled and dead, showing that water is the limiting factor for their growth and survival; also that the margin of safety for them is small.

All the diploid Cinnamomeae seem capable of forming tall, much-branched bushes and thickets by means of underground stems, the usual height being 6 to 10 feet. Under favorable conditions they bear flowers in corymbs on long lateral branches.

The Group of Rosa Woodsii Lindl.

The types belonging to the group of *R. Woodsii* have been tabulated in Table I according to the combinations of characteristics shown. These forms all have relatively narrow sepals, 2–3 mm. wide, which are usually eglandular. The sepals may be short (10–15 mm. long) and entire, or long caudate with 1–4 small lateral pinnae. The prickles are characteristically slender and terete. The roses of Utah and Nevada belong predominantly to this group. Scattered plants were also observed in the Sierra Nevadas of northern California, and in southern Oregon, as well as in the Mojave Desert and in southern New Mexico.

TABLE I

COMBINATIONS OF CHARACTERISTICS IN THE GROUP OF *Rosa Woodsii*

A. HIP GLOBOSE			
	a. Prickles straight		
Leaflet glabrous and eglandular	Leaflet pubescent	Leaflet pubescent and glandular	Leaflet glabrous and glandular
R. Woodsii	*R. Macounii*	*R. Fendleri*	*R. hypoleuca*
R. mohavensis	*R. ultramontana*		
	R. gratissima		
	b. Prickles deflexed or curved		
R. Woodsii	*R. puberulenta*	*R. adenosepala*	
	R. arizonica	*R. granulifera*	
	c. Unarmed		
	R. salicetorum		
	B. HIP PYRIFORM		
R. Woodsii	*R. pyrifera*	*R. neomexicana*	

In Utah

In the vicinity of Salt Lake City the forms *R. Woodsii* and *R. Macounii* Greene are very common along streams and ditches; the glandular *R. Fendleri* Crépin is infrequent.

The following variations were noticed in one group of plants along a creek with a distance of about half a mile:

Stems. — Almost unarmed. Green or reddish and glaucous. Prickles straight or curved on the same bush.

Leaflets.[1] — Narrow elliptic or ovate, broadly obovate or oval (sometimes on the same bush).

Hips. — Globose or with a slight neck or acute base. Small hips with many aborted achenes. Several vigorous bushes had aborted hypanthia and shriveled unopened flower buds, but no fruit.

Sepals. — A bush of *R. Fendleri* had small globose hips and short, spreading or reflexed sepals which were brittle and *partially deciduous.*

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[1] Note that this is the distinction used to separate *R. ultramontana* and *R. Macounii.*

The clump of *R. pyrifera* from which a seedling with sixteen chromosomes had been obtained (Erlanson, 4) was visited. The plants have glabrous foliage and resemble *R. Woodsii* in habit, with pyriform fruit. Some plants bore abundant hips, but others had a few small ones together with aborted hypanthia and dead unopened flower buds.

The aspen–spruce zone was visited in Summit County, Utah, and both diploid and hexaploid roses were found at an elevation of 7,000–8,000 feet. Among the diploids were *R. puberulenta* Rydberg and some almost unarmed *R. Macounii*, 3–4 feet high. At the end of September the latter bore small globose green hips with very few achenes or no fruit at all.

Pubescent branches

Some clumps of roses 4–5 feet high, in the mountains of Summit County, were noticed with all the young shoots and branches finely puberulent. Several of the hypanthia had aborted and the well-developed hips contained only a few achenes. The plants differed from *R. puberulenta* Rydberg chiefly in the puberulent stems and pedicels.

The character of pubescent twigs and pedicels has not been reported before in American diploid roses. It is characteristic of the Asiatic diploid *R. rugosa* and of the polyploid *R. Durandii* of Oregon. Flowering sprays of a diploid specimen with pubescent stems were seen in the herbarium of the California Academy of Science, collected at Bingham, Utah, by M. E. Jones in 1880. Later, on the shores of Lake Tahoe, Nevada, I found two clumps of *R. ultramontana* (S. Wats.) Heller, one of which had densely puberulent twigs and pedicels, and the other glabrous twigs and puberulent pedicels. This is a case in which Vavilov's idea of representing variations by a formula would be helpful in showing the actual relationship and make-up of these forms, which may not be identical, yet all of which possess this unusual characteristic.

In western Nevada

In Washoe County, Nevada, thick hedges of diploid roses 6–10 feet high grow along ditches and streams. Plants of *R.*

Fendleri and *R. Woodsii* were rare, but could usually be found in a large stand. *R. Macounii* was the commonest form. Many bushes had ellipsoid hips and would fall under *R. pyrifera* Rydberg. *R. salicetorum* Rydberg is a vigorous unarmed diploid, and is frequent along streams near Reno. Some of the unusual combinations of characteristics observed here were:

1. *R. Macounii*
   Leaflets almost glabrous, except the midrib
   Leaflets finely puberulent on both surfaces
   Achenes basally attached

2. *R. pyrifera*
   Leaflets almost glabrous
   Achenes mostly basal
   Prickles curved and straight on the same bush
   Unarmed (This might be called *R. salicetorum* with pyriform fruit)

3. *R. Fendleri*
   Prickles curved and straight on the same bush

On the eastern shore of Lake Tahoe there are many clumps of roses belonging to *R. Macounii* and *R. ultramontana*.[2]

In the arid sage brush country surrounding Pyramid Lake only two colonies of Rosa were discovered, both on the west shore of the lake. There were several large solitary thickets, 5–7 feet high, the stems armed with flattened, strongly curved prickles and bearing small solitary hips (many of which had been half eaten by birds). These isolated plants agree very well with the description of *R. granulifera* Rydb. They are stouter plants than the Arizona specimens of this form and are remarkable for the laterally compressed, hooked prickles. The leaflets are pubescent and glandular-granuliferous beneath with simple teeth.

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[2] *R. ultramontana* (S. Wats.) Heller and *R. Macounii* Greene (*R. grosseserrata* A. Nels.), as found in the Rocky Mountains and Sierra Nevadas, are separated by very unreliable characters. *R. ultramontana* has "elliptic or oval leaflets, usually rounded at both ends, dull green on both sides" (Rydberg, 9); *R. Macounii* has "leaflets obovate, usually cuneate at the base . . . pale beneath." Likewise, the former has petals "1.5 cm. long or a little more" and the latter "petals about 2 cm. long." Anyone who has studied rose cultures will know that these characteristics can be found intermingled on many individual bushes in Cinnamomeae. Rydberg (8) states that *R. ultramontana* "is closely related to *R. pisocarpa* and distinguished from that mainly by the sepals which are not at all glandular." Yet I have seen herbarium specimens in California with smooth sepals determined as *R. pisocarpa* by Dr. Rydberg, and quite correctly. *R. pisocarpa* is distinguished from the *R. Woodsii* group by its fine serrations and usually ascending prickles, its broader and shorter sepals and thin-walled hypanthia with rather small achenes. *R. ultramontana* (which *R. grosseserrata* A. Nels. also resembles) appears to be a geographical race of the group of *R. Woodsii* belonging to the Rocky Mountains, the Sierra Nevadas and to Oregon. *R. Macounii* was designated by Greene to refer to the lower, more bristly forms of the "dry elevated plains." In these notes I have continued to follow the nomenclature of the *North American Flora* (Rydberg, 8), since this is used by most students of Rosa.

All the roses seen in Nevada were apparently diploids belonging to the group of *R. Woodsii.*

In northern California and southern Oregon.

Beside the many shallow streams of the upper Feather River region, south of Mount Lassen, an abundant growth of diploid roses was seen. These belonged to the *R. Macounii* and *R. ultramontana* forms and were similar to those on the eastern slopes of the Sierra Nevada range. No plants were observed with glandular foliage. Several with pyriform hips would be classified as *R. pyrifera*, some of which were almost unarmed. *R. puberulenta* was collected and also a specimen which appeared to belong to the group of *R. californica* C. & S. The latter will be referred to below under tetraploid species.

No roses belonging to this group were observed in the upper Sacramento Valley nor around Ashland, Oregon. Near Jacksonville, Oregon, a group of completely unarmed plants, only 1–2 feet high, was found growing on a gravelly bank. The stems were stout and bore corymbs of large globose ripe hips on short lateral shoots on October 7. Those leaflets which had not fallen were ovate, pubescent and glandular-granuliferous beneath, and had coarse teeth. It was not possible to place it in any of the named forms, though it most nearly resembled *R. blanda* Ait. of the eastern United States.

Two bushes of *R. puberulenta* were found on a river bank in Medford, Oregon. One had corymbs of ripe hips full of achenes; the other, close by, had many aborted hypanthia and only a few full-grown hips.

In the arid Southwest

The group of *R. Woodsii* forms the characteristic diploid rose flora of the Rocky Mountains and of the Great Basin. It is also found far to the south in moist places in the arid regions. Two stations of *R. mohavensis* Parish were visited on the edge of the Mojave Desert at the foot of the San Bernardino Mountains. These plants are indistinguishable from *R. Woodsii.* The leaflets are small, of varied outline and not strikingly shiny. Some aborted flower buds were observed and a few solitary hips in mid-November; the rest had been eaten by birds.

In southern California, Arizona and New Mexico, where suitable habitats are very limited, one variety of Rosa may become established in a locality beside a spring and may soon fill all the available moist ground by the means of underground stems. Culture experiments are necessary to show whether or not isolation has resulted in the production of a true breeding race (Clements, 2; Hall, 5).

R. neomexicana Cockerell in the Membris Range of southern New Mexico resembles forms of *R. Macounii* with ellipsoid hips, as seen in the Great Basin. Other species which belong to this group and are found in isolated stations in the southwest are: *R. gratissima* Greene, *R. adenosepala* Wooton & Standley, *R. hypoleuca* Woot. & Stand., *R. arizonica* Rydb. and *R. granulifera* Rydb.

The Group of Rosa pisocarpa A. Gray

From the slopes of Mount Shasta and the Siskiyou Mountains, northward and westward, the rose flora has a very different aspect from that of the Sierra Nevadas and Great Basin. The diploid forms of Cinnamomeae here belong to the *Rosa pisocarpa* complex, and, except near Medford, Oregon, no specimens of the *R. Woodsii* group were observed.

The forms in this group have been tabulated in Table II. No specimens with glandular foliage have been found.

TABLE II

COMBINATIONS OF CHARACTERISTICS IN THE GROUP OF *R. pisocarpa*

PRICKLES STRAIGHT

a. Hip globose

Leaflets glabrous	Leaflets pubescent	Leaflets glandular
	R. pisocarpa	
	Unarmed	
	R. anacantha	
	b. Hip pyriform	
R. Copelandii	*R. Eastwoodiae*	
	Unarmed	
	R. Pringlei	

The following unusual combinations of characters were observed:

1. *R. pisocarpa*
   Foliage glabrous
   Foliage glabrous except on the midribs
   Almost unarmed, hips variable in shape
   Sepals glandless
   Sepals eglandular, pubescent
2. *R. Copelandii*
   Almost unarmed
   Sepals gland-hispid
   Rhachis of leaflets pubescent
3. *R. Pringlei*
   Hips solitary
   Sepals and pedicels glandular hispid
   Sepals reflexed, pedicels glandular
   Leaflets almost glabrous

Local Variations

In some localities unusual and local forms of Rosa are present. This was most striking in Ashland Cañon, Oregon. For about two miles along a moist, semishaded, rocky defile many rose bushes related to *R. pisocarpa* A. Gray were growing. The effect of the shade and moisture seemed to be to increase the size of the plants and to render them nearly sterile. Many of the bushes were 10–12 feet high, with weak slender stems and branches and only a few solitary hips. The majority had pyriform or urceolate pendent hips, glandular-hispid sepals and almost glabrous foliage. They did not fit into any of the named forms. Such variants should be named if they breed true and retain their anomalous characteristics when transplanted to an experiment garden.

In the Willamette River Valley

In Oregon in October a visit was fortunately made to Corvallis, where Professor H. M. Gilkey kindly took me where wild roses were most abundant. In one lane there were continuous hedges of wild roses for a distance of over half a mile. They belonged to the *R. pisocarpa* group intermixed with a good many polyploid relatives of *R. nutkana.*

The four forms, *R. pisocarpa, R. Eastwoodiae* Rydberg, *R. Copelandii* Rydb. and *R. Pringlei* Rydb., were found and some with anomalous combinations of characteristics. Plants of *R. Pringlei* were very vigorous, 6–8 feet tall, with large compound corymbs of hips on lateral branches and sepals densely glandular-hispid. A similar plant on the Willamette River, with hips 1–3 together, had leaflets which were glaucous and almost glabrous beneath.

Rosa pisocarpa × hexaploid species

Two large bushes were found in the lane near Corvallis, one of which produced almost entirely aborted hypanthia and the other about fifty per cent of aborted fruit. The plants both had the habit and armature of *R. nutkana,* but the inflorescence was corymbose. Both had glandular sepals and leaflets resembling those in *R. pisocarpa,* but conspicuously glandular-granuliferous beneath. The bush, which had about half of its fruits developed, had the young branches finely puberulent and glandular, as in *R. Durandii.* The latter, which is probably hexaploid, grew close by. These sterile and semisterile bushes are suspected of being *R. pisocarpa × Durandii.* A specimen from Montana was referred to *R. nutkana*

× *pisocarpa* by Rydberg (9), who says nothing about the amount of good fruit.

On the Pacific Coast

A few clumps of *R. pisocarpa* were observed in the Coast Range west of Corvallis. Along the Pacific Coast near Newport, Oregon, the flora is rich in Ericaceae and no roses were found.[3]

The southern coast of Oregon was not visited, but at Crescent City, Del Norte County, California, diploid and hexaploid roses are common, as soon as one descends from the Sequoia-covered slopes to the alluvial flats. The diploid roses here are typical *R. pisocarpa* and *R. Pringlei.* These species were not seen south of Crescent City. The coast here is edged by cliffs and roses should be looked for on alluvial land in river estuaries.

Rosa gymnocarpa Nuttall

R. gymnocarpa Nutt. was first seen in northern California near Mount Eddy. It is a quite variable species, yet all attempts at splitting it into many species have failed. It is remarkable among American roses for being shade-tolerant. The Cinnamomeae are often unable to set a normal amount of fruit even in semishaded situations. The most flourishing and fructiferous bushes of *R. gymnocarpa* seen were partially shaded. Plants growing in the open and on dry mountain sides were usually stunted and almost devoid of hips.

This species has completely glabrous large achenes (5 mm. long by 3 mm. thick) and there are only from one to seven in each hip. Bushes were observed in which every hip was ellipsoid with a distinct neck, regardless of the number of achenes, so that hip shape is not always dependent, as Rydberg (8) suggested, upon the number. In semishade some plants were found with hips 10 mm. in diameter and as much as 15 mm. long.

The time at which the calyx and styles are shed varies a great deal. On some bushes, in the interior of California, the sepals were reflexed on large ripe hips in October, while on others they had all fallen.

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[3] *R. rubiginosa* L. is common as an introduced weed in meadows in Oregon. In favorable habitats it may reach gigantic proportions; bushes over fifteen feet high were seen near Medford.

A graceful bush nearly 5 feet high, on the lower slopes of Mount Eddy, agreed with the diagnosis of *R. dasypoda* Greene, except that it had large ellipsoid hips.

R. gymnocarpa is common throughout the Siskiyou Mountains and is found at the border of woods in the Willamette Valley at only 300 feet above sea-level. It is the only rose associated with the Sequoia, growing in openings in the forests. It was observed on Mount Tamalpais, Marin County, California, and on the hills near Berkeley. No plants with pubescent leaflets were found throughout its range. This variation is rare.

Rosa stellata Wooton

The type locality of *R. stellata* Wooton was visited in New Mexico. Here clumps of low bushes grow scattered over about half an acre of mountain side. Most of the bushes had only aborted hypanthia and, after a careful search, only one hip was found containing achenes.

THE HEXAPLOID ROSES

The hexaploid roses seen on this trip were all related to *R. nutkana* Presl. This complex is made up of the following forms tabulated in Table III, as well as other unnamed combinations of variations. They are all characterized by having well-developed paired infrastipular prickles, the flowers solitary or two or three together, and large thick-walled hips containing from forty to fifty large pubescent achenes 4–5 mm. long.

It will be noticed that in this group glandular foliage predominates. Any of the forms may have glandular pedicels and sepals.

Hexaploid roses in Utah

In Summit County, Utah, both *R. oreophila* Rydb. and *R. Spaldingii* Crépin were found at an altitude of between 7,000 and 7,500 feet.

TABLE III

COMBINATIONS OF CHARACTERISTICS IN THE GROUP OF _R. nutkana_

The species marked with an asterisk (*) have not been examined cytologically as yet. They are considered by taxonomists to be related to _R. nutkana_ (Rydberg, 10) and they resemble American hexaploid species in fundamental morphological characteristics.

HIPS GLOBOSE

a. Prickles straight

Leaflets glabrous and eglandular	Leaflets pubescent and eglandular	Leaflets pubescent and glandular	Leaflets glabrous and glandular
*Unnamed type from Mt. Shasta City	_R. Spaldingii_	_R. nutkana_ *_R. Brownii_ (Dwarf = *_R. yainacensis_)	_R. muriculata_
b. Prickles curved			
R. melina	*_R. oreophila_	*_R. columbiana_ (a dwarf is *_R. myriadenia_) Branches pubescent *_R. Durandii_	_R. manca_

R. oreophila has not been examined cytologically, but it has the characteristics of a hexaploid. The bushes were about one meter high and at the end of September the solitary, pendent hips had already ripened and dried, showing that the plants had bloomed early. _R. Spaldingii_ was found a few hundred feet higher up the mountain among the aspens. It bore solitary hips which were colored, but not yet soft. Some plants of the latter species had deflexed prickles and glandular-hispid pedicels.

Group of Rosa nutkana in Mount Shasta region

The roses seen near Mount Shasta with the habit of hexaploids were all closely related to _R. nutkana._ A plant was found near the base of Mount Eddy with perfectly glabrous and eglandular foliage and simple teeth. This is an undescribed variety of _R. nutkana,_ which belongs in the space in the first column of Table

III. One giant plant of *R. nutkana* was found on a semishaded stream bank, which was eight or nine feet tall with several aborted hypanthia, as well as green well-developed hips, which, however, contained many aborted achenes as well as some with embryos. The semisterility may have been due to lack of light.

According to Rydberg (8), *R. Brownii* Rydb. is the commonest form of the group of *R. nutkana* in this region. I found plants that agreed with his description of *R. Brownii;* others were typical *R. nutkana.* Still others had stout ascending prickles like *R. nutkana* and leaflets finely puberulent beneath; these would be classed as *R. Brownii* from the leaflets, and as *R. nutkana* from the prickles. This is another example of the inadequacy of the current method of segregating species on the basis of characters which may be combined in every possible way and may even vary on one and the same individual.

Many of the plants of *R. nutkana,* both near Mount Shasta City and in Del Norte County, California, had the sepals spreading and reflexed on the mature hips.

In the Willamette River Valley

The hexaploid roses near Corvallis belonged to the group of *R. nutkana,* many different varieties and combinations of which were found. The hedgerow mentioned above, in which the sterile hybrid bushes were growing, also contained *R. Durandii* Crépin, typical *R. nutkana* and the form with glandular-muriculate leaflets, *R. muriculata* Greene. One large clump of the latter had many solitary, ellipsoid hips, acute at the base and with short necks. A pyriform fruited form has not been reported heretofore in this group. Dr. W. E. Lawrence, of the Oregon Agricultural College, collected the same form near Skelton, Washington.

The rare *R. Durandii* has branches and turions puberulent and finely glandular. The stout, flattened prickles are also finely puberulent and, on the Oregon plants, varied from curved to straight. The foliage of *R. Durandii* is coarse with oval, rugose leaflets which are pubescent and glandular-granuliferous beneath. It has the habit and inflorescence type of a hexaploid and belongs, apparently, to the group of *R. nutkana.* The foliage resembles that of the Gallicae rose species, which, under Dr. Hurst's scheme, are AACC tetraploids. *R. Durandii* may happen to be one of the missing hexaploids, AACCDD or AACCEE[4] (Hurst, 6). This species is represented in very few herbaria; the only specimens seen by the writer are Elihu Hall's original specimens from "Oregon," collected in 1895. Rydberg (9) reports only two other collections, both from the valley of the Willamette River. Rydberg also doubtfully refers two other specimens to this species because they possess pubescent branches.

Rosa nutkana on the coast of northern California

The group of *R. nutkana* grows along the coast in northern California in alluvial soil. At Crescent City both *R. Brownii* and *R. muriculata* were collected.

At Eureka there are colonies of normal *R. nutkana* and also a few with bristly fruits resembling *R. MacDougali* Holz. (*R. nutkana* var. *hispida* Fernald) of the northern Rocky Mountains. These plants were not encountered when I was at Eureka, but herbarium specimens were seen at the University of California and the collector, Mr. J. P. Tracey, kindly sent me ample fruiting specimens of both forms. Mr. Tracey wrote that "the prickly-fruited ones are from a colony which occupies a space of about twenty square feet. It is surrounded by the usual smooth-fruited form, which is abundant in the locality. I believe that all the prickly-fruited colony here is developed from one original plant." He has also collected specimens with bristly fruits at Alton, south of Eureka.

The normal *R. nutkana* from Eureka had achenes 3.5–4 mm. long and from 30 to 45 in each hip. The form resembling *R. MacDougali* had achenes 6–7 mm. long and only one to eight had developed in each hip, though many of the hips were globose and a centimeter in diameter. If this form is also highly pollen-sterile, it would seem to be an example of a mutation which causes sterility as well as hispid hypanthia. Such a phenomenon will further complicate the detection of wild hybrids in Rosa by the criterion of pollen sterility.

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[4] Hurst thinks that there are only five primary diploid groups or species in Rosa, each of which possesses a "double septet" (seven pairs) of chromosomes and which he designates as AA, BB, CC, DD and EE species. The polyploid forms, under this scheme, are made up of various combinations of the characters and chromosomes of the five diploid species, the chromosomes of each "septet" always remaining together.

R. muriculata, with the turions densely setaceous, as well as prickly, was collected in October, 1928, along the coast six miles south of Casper, Mendocino County, by H. L. Mason and Lucile Roush. Hexaploid roses may, therefore, range farther south on the Pacific Coast than is shown in my distribution map (Erlanson, 4).

TETRAPLOID ROSES

The Group of Rosa californica

Roses of the West in the group of *R.californica* are tetraploid and are almost entirely confined to California and Lower California. Occasional plants may be found in southern Oregon (Rydberg, 9) and on the eastern slopes of the Sierra Nevadas in Nevada.[5]

The roses in the group of *R. californica* are all characterized by possessing well-developed infrastipular prickles and short pedicels. The flowers are usually borne in corymbs on long lateral branches and flowering turions may be produced under favorable conditions. The named forms and varieties have been tabulated in Table IV.

In northern California in the interior

A single plant agreeing with the diagnosis of *R. myriantha* Carr., as given by Rydberg (9), was found beside a stream in Plumas County at an altitude of about 4,700 feet. It had no flowering turions, but otherwise resembled specimens from Nevada City, California, which were grown at the Botanical Garden of the University of Michigan and were found to be tetraploid (Erlanson, 4). These are interesting forms since, in some respects, they appear to be intermediate between *R. californica* C. & S. and such diploid species as *R. puberulenta* and *R. pyrifera.*

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[5] A herbarium specimen of *R. rotundata* Rydberg, from the type locality, Franktown, near Reno, was seen in the herbarium of the Nevada Agricultural Experiment Station. It is a flowering specimen, but seems to me to belong to the group of *R. californica,* being nearest to *R. myriantha* Carr. Tidestrom (11) gives the range of *R. rotundata* as "western Nevada and California."

R. californica was observed in the Sacramento Valley at Redding, but not in the Mount Shasta region nor in southern Oregon.

TABLE IV

COMBINATIONS OF CHARACTERISTICS IN THE GROUP OF *Rosa californica*

Leaflets glabrous-eglandular	Leaflets pubescent-eglandular	Leaflets pubescent-glandular	Leaflets glabrous-glandular
A. HIPS URCEOLATE OR ELLIPSOID			
a. Prickles curved			
	R. californica	*R. Aldersonii* *R. Greenei* *R. Breweri*	
b. Prickles straight			
R. myriantha	*R. myriantha*		
B. HIPS GLOBOSE			
a. Prickles curved			
		R. brachycarpa	
b. Prickles straight			
	R. Johnstonii *R. rotundata* ? *R. corymbiflora*	*R. Dudleyi* *R. Santae-Crucis*	*Dwarf* ? *R. spithamea*

On the coast of California

This group of roses is adapted to arid habitats, but many plants were observed that seemed to be suffering from desiccation. The scarcity of water gives a scattered distribution to *R. californica* and nowhere, in the regions visited along the coast, is it as abundant as are the diploid species in the Great Basin.

Flowering turions were seen in Marin County and San Bernardino County. They are not as frequent as on the tetraploids of the great plains east of the Rocky Mountains. Hurst (7) has pointed out that perpetual flowering and dwarf habit are usually linked in Rosa. *R. californica* affords an example of occasional perpetual flowering in a tall form.

The characteristics separating the different forms as used by Greene and Rydberg are all quite variable and may be variously combined. Individuals of *R. californica* were found on which some prickles were straight and others curved; some hips were almost globose and others had a distinct neck. Pubescent or glandular pedicels are frequent in this group. All the tall forms seem to be closely related to one another. Plants were found near Berkeley and also in the south in San Bernardino County, with many aborted hypanthia. In the southern specimens this may be partially due to the drought.

There are several interesting forms of limited range which appear to be related to this group, such as *R. calavera* Greene, *R. pinetorum* Heller and *R. spithamea* S. Wats. The only specimen I collected was *R. spithamea* var. *sonomensis* Jepson on Mount Tamalpais. The cytology of these forms might throw some light upon the origin and relationships of the western tetraploid roses.

R. pinetorum is in some respects intermediate between *R. nutkana* and *R. californica.*

SUMMARY

1. The recurring variations observed in five large groups of wild roses in Utah, Nevada, Oregon and California are enumerated.
2. The combinations of these variations have been tabulated in an attempt to give the numerous named forms their respective values. The species have been grouped under *R. Woodsii, R. pisocarpa, R. gymnocarpa, R. nutkana* and *R. californica.*
3. Some unusual combinations of characteristics were found, but a further multiplication of specific names is considered inexpedient until the relationships of the forms are better understood.
4. The species within each group or collective species appear to be "hybrid swarms" and not true cases of parallel variation.
5. Roses belonging to the group of *R. Woodsii* with puberulent branches were found in Utah and Nevada.
6. *R. Durandii* was found near Corvallis, Oregon; also two

semisterile bushes which appeared to be *R. pisocarpa* × *hexaploid.*

7. Excessive drought or insufficient sunlight may prevent normal fruit production in some roses. *R. gymnocarpa* is shade-tolerant.

8. A pyriform fruited plant in the group of *R. nutkana* was found in Oregon. Another form with hispid fruits like *R. MacDougali*, but semisterile, is reported from Eureka, California.

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THE PHENOLOGICAL PROCESSION IN NORTH AMERICAN WILD ROSES IN RELATION TO THE POLYPLOID SERIES *

EILEEN WHITEHEAD ERLANSON

FOR the past three years notes have been taken on the time of flowering of the wild roses in the large assemblage of native forms at the Botanical Garden of the University of Michigan, and some interesting facts have become apparent. The data have been plotted in three charts, one for each year, and are arranged under well-defined species groups. In 1926 notes were taken on 160 individuals or collections, in 1927 on 240, and in 1928 on 270.

The individuals belonging to each species group have been arranged with reference to their wild origin, those collected in more northern stations being placed first and those from southern stations last. The charts are not reproduced here. They bring out clearly that the order of entering anthesis does not indicate the existence of races differing in flowering period in any of the species under observation, with the possible exception of *Rosa palustris* Marsh.

Time of flowering is a good specific character, the initial date for which in a given season usually falls within a ten-day period for all indivduals of any of the larger species groups. Those plants which come into flower late, with reference to their relatives, often have a short flowering period and cease at the same time as those that began earlier.

Variations such as those with glandular, pubescent or glabrous

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TABLE I

PHENOLOGICAL DATA FOR ROSES CULTIVATED AT ANN ARBOR, MICHIGAN

Group or Species	Flowering began			Last flower			First ripe hips
	1926	1927	1928	1926	1927	1928	
HEXAPLOID							
R. acicularis..	May 30-June 8	May 22-June 1	May 27-June 7	June 27	June 22*	June 21*	Second week of July
R. nutkana...	June 8-14	June 1-10	June 8-14	June 30	June 28	June 26	End of Aug.
DIPLOID							
Cinnamomeae							
R. blanda....	June 9-18	June 3-12	June 9-14	July 3†	July 2†	July 4†	Middle of Aug.
R. Woodsii...	June 10-15	June 5-15	June 9-18	July 4	July 1	July 1	First wk. of Aug.
				End of main flowering			
TETRAPLOID							
R. arkansana	June 18-30	June 10-22	June 19-25	July 16	July 13	July 14	Third wk. of Aug.
R. rudiuscula	June 21-27	June 15-25	June 23	July 18	July 12	July 13	Fourth wk. of Aug.
R. virginiana	June 23-30	June 16-27	June 19-30	July 18	July 14	July 14	Third wk. of Aug.
R. carolina...	June 24-July 6	June 18-July 4	June 22-July 4	July 20	July 15	July 14	End of Aug.
R. californica		July 5-8	July 11-18		Aug. 7	Aug. 9	Mid-Sept.
DIPLOID							
Carolinae							
R. palustris..	July 7-20	July 3-18	July 6-20	Aug. 10	Aug. 9	Aug. 9	First wk. of Oct.
Synstylae							
R. setigera...		July 6-14	July 7-15		Aug. 5	Aug. 7	End of Sept.

* Except 3511

† Except 2686

foliage, globose or pyriform hips, show no distinct correlation with regard to early or late flowering.

The time when the hips begin to soften has been noted approximately for each group, not individually for each collection, and will be found in the last column of Table I. This table is a synopsis of the data for each group of species during three years and Figure 2 is the same thing expressed graphically, with the successive peaks of maximum flowering activity shown.

If the flowering periods of all the species groups, assembled under uniform conditions, are compared, it appears that those groups in the most northerly range bloom first. The only octoploid *Rosa acicularis* Lindl. in the garden flowers well in advance of all other roses. These plants came from central Alaska. Little is known of the range of the octoploid race, though it is no doubt arctic and subarctic.

Rosa nutkana Presl has been collected along the Alaskan coast. It is a hexaploid ($2n = 42$) and begins to flower a few days earlier than the diploid Cinnamomeae. The hexaploid group of *R. acicularis* (vars. *Sayiana*, *Bourgeauiana*, etc., and *R. Engelmanni*) is represented in the northern Rocky Mountains; it begins to flower about a week before *R. nutkana.* I have suggested (Erlanson, 4) that the hexaploid *R. acicularis* group in America may have arisen from crossing between octoploid *R. acicularis* and hexaploid *R. nutkana.* The flowering periods of known interspecific hybrids in our garden are intermediate between those of the parents.

Rosa blanda Ait. ($2n = 14$) belongs to the northeastern part of the American continent, ranging north to the southern parts of Hudson Bay. It comes into flower when the hexaploid *R. acicularis* has reached the peak of flowering activity and is at a maximum when the latter is about over. The flowering period of the diploid western species of the group of *R. Woodsii* Lindl. is the same as that of *R. blanda.*

Among the American tetraploid species the group of *R. arkansana* Porter ranges farthest to the north and begins to flower first.

The range of *R. palustris* is on the whole southern and it flowers in July together with the late-flowering southern species *R. californica* C. & S. and *R. setigera* Michx.

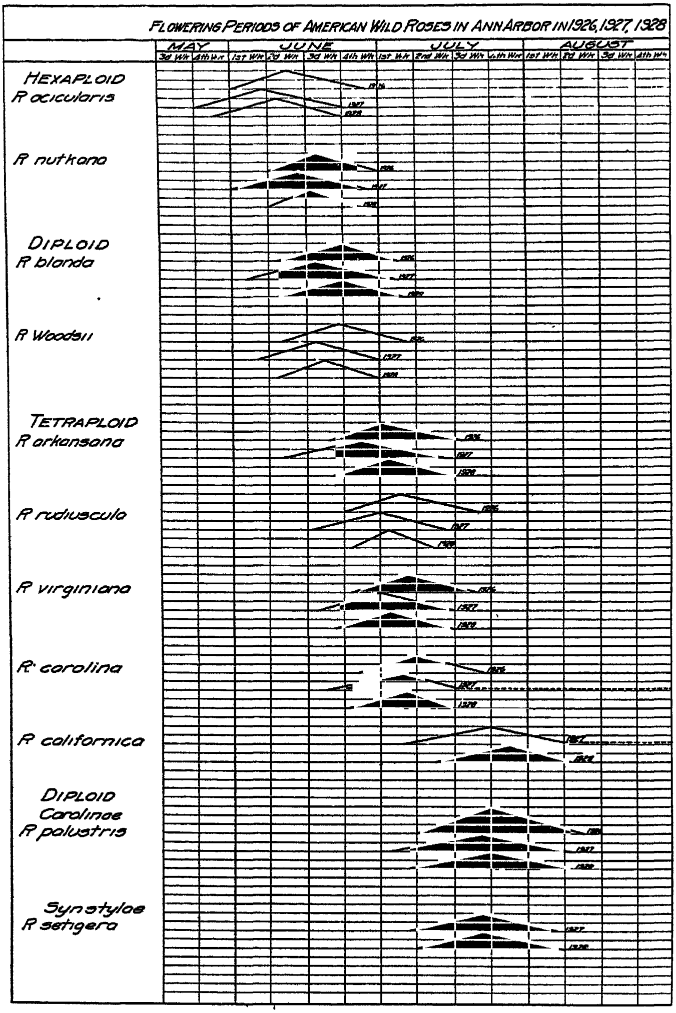

FIG. 2. The flowering periods of some collective species of Rosa at Ann Arbor, Michigan, for 1926, 1927 and 1928. Each flowering period is plotted as a curved line in which the date of maximum flowering acitivity is indicated by the peak. The first column contains the names of the species or groups studied; these have been placed under their cytological class

There are very few published data on the phenology of the other polyploid genera. Hedrick (6) states that *Prunus hortulana* and *P. Munsoniana* are the latest to come into bloom in New York. Both are southern forms.

Darlington (1) gives an interesting list of the dates of maximum activity in pollen mother cell division in Prunus. The earlier species are all diploid, the aneuploid, hexaploid and tetraploid forms beginning their activity later. In Rosa meiosis does not occur in the anthers until the flower buds appear between the stipules of subtending leaves, so that the maximum activity for maturation roughly coincides with the appearance of the first flower, or precedes this by a day or two only. The higher polyploids in Rosa seem to be unique in their early flowering and in the regularity of their meiosis (Erlanson, 4). If the octoploid and hexaploid species are disregarded, the order of flowering of the cytological groups in Rosa is similar to that in Prunus; first diploids, then tetraploids, the latter being followed by southern diploids. The tetraploids may be of relatively recent origin, corresponding to the tetraploids in Prunus and other genera, while the higher polyploids seem to have attained their condition much earlier.

As I have pointed out before (4), there seems to be some correlation between primitiveness and early flowering in Rosa. Harshberger (5) and Illitschevsky (8) have shown that the majority of vernal-flowering species are primitive. It would be interesting to find whether this is also true for the species within large genera.

It is remarkable that there seems to have been no selection within the species groups of early and late flowering races in the northern and southern parts of their wide ranges. These races, when present, seem to be due to hybridization between two groups (see below under "*R. blanda*" and "*R. palustris*").

It is shown in Figure 2 that 1927 was an early season. Most plants came into flower about six days earlier than in the other two years. In 1927 there was a tendency for the individuals within some groups to enter anthesis more unevenly than in the other years. This was most noticeable in the group of *R. carolina*.

Several plants of *R. acicularis* continued to produce a few flowers on short laterals for a week after their main flowering period was over. One plant of *R. acicularis* var. *lacorum* Erlanson had a second blooming in October, 1927. Usually all the early flowering roses have a definite and circumscribed flowering period of about a fortnight for each individual, after which they cease to produce any more flower buds. Flower production in 1927 did not cease earlier than in the other seasons. This indicates that in early or mild years the period of anthesis is longer; there is more overlapping between different groups, and hence more chance for cross-fertilization to take place between them. In 1928 the weather was dry and hot in June and *R. carolina* L. and allied forms, which began to flower during the last week of that month, were almost through in ten days. The important factor in preventing further flower production thus seems to be the rise in temperature usual during July in Michigan.

Individual plants flowering first in their group one season may not always do so. There are, however, some constantly early or late-flowering plants and these have often turned out to be new forms or to have cytological disturbances and much sterile pollen, phenomena pointing to a hybrid origin.

OCTOPLOID ROSES

We have only one collection of *Rosa acicularis* which is known to be octoploid ($2n = 56$). These plants, which were sent from Fairbanks, Alaska (Bot. Gard. No. 6447), flowered in 1926 from May 22 to 29 and in 1927 from May 17 to 31. In 1928 they were damaged by frost in May and produced no flowers. The hips of these plants are ripe early in July.

HEXAPLOID SPECIES

With hexaploid *R. acicularis* are grouped the allied forms *R. Engelmanni* S. Wats., *R. Underwoodii* Rydb., *R. manca* Greene and the varieties *lacorum*, *Sayiana* and *rotunda* of *R. acicularis* described by the writer in 1925 (Erlanson, 2). Vars. *Bourgeauiana* Crépin and *rotunda* have a tendency to begin flowering a few days after the pyriform-fruited varieties. This tendency is not to be absolutely relied upon, however, since in 1928 in a mixed culture (No. 2592) var. *lacorum* began to flower three days later than var. *Bourgeauiana.*

Collections of *R. acicularis* var. *Sayiana* from Alcona, Michigan (No. 6294), near the southern limit of the species in Michigan, from McGregor Bay, Lake Huron, Ontario (No. 5668), and from Mackinac County, Michigan (No. 3754) are all constantly early in beginning to flower.

Plants of *R. acicularis* var. *rotunda* from Cheboygan County, Michigan (No. 3511), have a longer flowering period than the average; flowers continued to be produced for over three weeks in 1927 and 1928.

One plant of *R. blanda* var. *glandulosa* Schuette in a collection from Mackinac County, Michigan (No. 3753), did not flower until it was four years old in 1927. That season it bore three flowers at the time when the *R. acicularis* group was blooming. In 1928 it flowered first on May 31; the other plants of the culture commenced June 13–15. This plant is now being studied cytologically. It has never set any fruits and has over 75 per cent dwarf pollen grains.

Rosa nutkana and its relatives are not numerous in our collection; notes have been taken on eight accessions only, as compared with thirty-two in the group of *R. acicularis*. *R. nutkana* begins to bloom when the group of *R. acicularis* is at its maximum flowering activity. *R. Spaldingii* Crépin from Kalispell, Montana (No. 6080), was a seedling with only three flowers in 1927; in 1928 it flowered a week earlier than any other plant in this group. *R. Spaldingii* from Rimrock, Washington (No. 5298), comes into flower relatively late. This group is characterized by being tardy in ripening its fruit. The earliest hips do not soften until late in August, and not until late September in *R. muriculata* Greene.

The fruit of the hexaploid forms of *R. acicularis* ripens relatively rapidly—in six weeks after the initiation of flowering. This is to be expected in a boreal and arctic species. In the other groups of species the average time for ripening of hips is from eight to ten weeks.

DIPLOID CINNAMOMEAE

Under *R. blanda* have been grouped the varieties of that species, together with *R. subblanda* Rydb. and *R. acicularioides* Schuette. The simultaneous appearance of first flowers on plants from widely separated stations is very striking in this group. In 1927, among forty-four collections from many parts of the range of the species, eighteen began to flower on June 7–8. In 1928, out of forty-three collections, twenty-four, more than half, began to flower on June 13–14. Two cultures of var. *hispida* Farwell from Winnipeg, Manitoba (Nos. 5771 and 5773), are always among the first, but there are plants from Illinois that are as early as they, though more variable. Var. *hispida* from Des Plaines, Illinois (No. 2656), was early in 1928 (compared with the group as a whole), though not in other years. *R. blanda* from Livingston County, Michigan (No. 3942), near the southern limit for the species in Michigan, is always late in coming into flower and does not bloom for long. *R. subblanda* from near St. Louis, Missouri (No. 4581), does not deviate from the rest of the group. A collection from Houghton County, Michigan, always produces its first flowers after all the others in this group are flowering. This was described (Erlanson, 3) as *R. blanda* var. *Hermanni*, and is intermediate in some characteristics between *R. blanda* and *R. palustris*. It has a longer flowering period than most specimens of *R. blanda;* it flowered from June 18 until July 8 in 1926; from June 15 until July 12 in 1927; and from June 20 until July 18 in 1928. Var. *Hermanni* from Luce County, Michigan (No. 2668), is not so pronouncedly late as the type collection.

The diploid hybrid *Rosa Tetonkaha,* produced by Professor N. E. Hansen from *R. blanda* × *R. rugosa* hyb., flowers with the two parent species.

The western diploid species in the group of *R. Woodsii,* including *R. Macounii* Greene, *R. Fendleri* Crépin, *R. hypoleuca* W. & S., *R. puberulenta* Rydb., and *R. pyrifera* Rydb., flower synchronously with the group of *R. blanda,* showing more irregularity in coming into bloom. In 1926 and 1927 the culture of *R. pyrifera* from Utah (No. 6610), in which a plant with sixteen chromosomes was found (Erlanson, 4), began to flower among the last of this group. It bore no flowers in 1928. The hips of *R. Woodsii* ripen two weeks or more before those of *R. blanda.*

The western diploid species belonging to the group of *R. pisocarpa* A. Gray do not thrive in the dry hot Michigan summer and are also cut back by our winters. They are represented in the Botanical Garden by only four accessions and these have begun to flower at the end of June, a little later than most of the other diploid species. The same thing is true for *R. gymnocarpa* Nutt., which has bloomed only twice (at the end of June) at Ann Arbor.

TETRAPLOID SPECIES

The tetraploid American roses are characterized by the ability to produce flowers on the season's turions or surculi. The first flowers are borne on lateral branches on the old wood, as in the earlier roses, and after about a fortnight flowers cease to be produced on the main stems. Flowering turions may be produced throughout the summer, though always sparingly. These herbaceous shoots sometimes branch under the first terminal inflorescence and produce additional buds at the tips of one, two or three lateral branches.

Eastern tetraploid species, from east of the Rocky Mountains, include the group of *R. arkansana,* with *R. arkansana, R. suffulta,* Greene, *R. polyanthema* Lunell, *R. Bushii* Rydb., *R. subglauca,* Rydb., *R. ratonensis* Erlanson and *R. relicta* Erlanson; *R. rudiuscula* Greene; *R. virginiana* Mill; and the group of *R. carolina* with *R. carolina, R. serrulata* Raf., *R. Lyoni* Pursh, *R. obovata* Raf., *R. nanella* Rydb., *R. subserrulata* Rydb., *R. petiolata* Rydb., *R. Palmeri* Rydb. and *R. Deamii* Erlanson.

The *R. arkansana* complex is the first of the tetraploids, by a few days, to begin flowering. The plants show much variation among themselves in this respect, not synchronizing as well as those in the group of *R. blanda.* Likewise, an individual that is early one year may be late the next year. One plant in the early-flowering collection of *R. blanda* var. *hispida* from Winnipeg (No. 5771) was originally segregated because it flowered about ten days after the others. It was found to be a tetraploid resembling a tall *R. arkansana*. *R. relicta,* from northeastern Illinois (No. 8320), is semisterile and always flowers among the first of the tetraploids. *R. Bushii* from Courtney, Missouri (No. 3080), is also one of the earliest in this group.

R. rudiuscula the writer believes to have originated from *R. carolina* × *suffulta*. It is not easy to distinguish and begins to flower with the last of the *R. arkansana* group and among the first of the *R. carolina* group.

R. virginiana, coming into bloom with *R. carolina,* is also among the earlier tetraploid types. Seedlings from Orono, Maine (No. 4476), have been the first *R. virginiana* each year to begin flowering; they are aberrant morphologically, being nearly unarmed and with eglandular hypanthia.

The sterile triploid hybrid *R. virginiana* × *diploid sp.*, from North Carolina (No. 2872), flowers among the first in the *R. virginiana* group, which indicates that the diploid parent may have been *R. blanda* and not *R. palustris,* as suggested in 1929 (Erlanson, 4).

R. carolina and its relatives reach the peak of flowering activity during the first days of July. Among the latest to commence blooming are plants from Massachusetts and also some from Missouri. *R. Deamii* is one of the earliest of this group, as is *R. petiolata* from southern Missouri (No. 3669). *R. Lyoni* seems to begin flowering a few days later than most of the other forms; at least none of these plants are among the earliest. A collection of *R. carolina* from Hopedale, Illinois (No. 4529), consists of dwarf and tall plants. Each season the dwarfs begin to flower from three to six days before the taller plants.

Two collections of *R. subserrulata* from Arkansas were examined cytologically and one was unexpectedly found to have only fourteen somatic chromosomes; the other was tetraploid with twenty-eight (Erlanson, 4). The two forms scarcely differ in the time when first flowers appear. In 1927 the tetraploid bloomed six days earlier then the diploid, and in 1928 two days earlier.

The fruiting triploid rose from New York (No. 2949) begins to flower each year with the earliest of the *R. carolina* group. It is probably *R. carolina* × *blanda.*

TABLE II

Dates of Flowering of *Rosa palustris* and Allied Types in 1927

A cross (×) indicates the date when flowering was initiated. In three places a straight line marks the entire flowering period. An asterisk (*) marks the flowering dates of a culture which contained a triploid plant and of the triploid itself.

Species and wild origin	June										July																						
	21	22	23	24	25	26	27	28	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
R. michiganensis...																																	
Michigan																																	
Cheboygan Co..	×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—															
R. Schuettiana.....																																	
Michigan																																	
Cheboygan Co..				×	—	—	—	—	—	—	—	—	—	—	—	—	—	—															
R. palustris × rugosa No. 5494........							×																										
R. palustris × ? carolina No. 5590																																	
New Jersey......															×*																		
R. palustris																																	
Ontario, No. 5854.													×																				
Michigan																																	
Cheboygan Co..																	×																
Boyne City....																	×																
Glen Haven...																			×														
Grand Traverse Co..........																	×																
Grand Traverse Co..........																		×															
Midland Co....																			×														
do.																				×													
do.																				×													
No. 5714 Tuscola Co......					×	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—			
Washtenaw Co.																					×												
do.																						×											
New York																																	
Erie Co........																						×											
Onondaga Co...																									×								
Indiana																																	
St. Joseph Co..																												×					
Elkhart Co....																						×											
Wells Co......																											×						
Ohio																																	
Lorain Co.....																									×								
do.																												×					
Delaware Co...																												×					
New Jersey																																	
Lebanon 5590..																							×*										
Maryland																																	
Pr. Georges Co.																								×									
Virginia																																	
James City Co.																			×														

A weak plant from Illinois, agreeing with the description of *R. Palmeri* (No. 9516), always blooms among the last of this group.

Rosa californica growing in Michigan comes into flower late, beginning the first or second week in July. It continues to produce flowers until frost.

DIPLOID GROUP OF ROSA PALUSTRIS

The recently described species *R. michiganensis* and *R. Schuettiana* (Erlanson, 3) are diploids from northern Michigan which come into flower with *R. carolina*, about two weeks before *R. palustris*, and are through by the middle of July. It is thought that they may be descendants of crossing between *R.palustris* and the earlier-flowering *R. blanda.*

Rosa palustris is the only species, among those studied, which shows some indication of an early-flowering geographical race. This species grows in acid swamps, also along lake shores and streams in heavy soil. In the Botanical Garden at Ann Arbor it is growing in a sandy loam soil, yet most of the transplants and seedlings thrive, forming large bushes which flower profusely. Table II is a portion of the phenological chart for 1927, showing the time of appearance of first flowers in *R. palustris* collections and related diploid species. Data are given for large healthy bushes only. The plants from Michigan are the earliest, those from the northern part of the state beginning before those from the central and southern parts. Collections from farther south begin later, except plants from Williamsburg, Virginia (No. 3164), which always begin to bloom as early as those from Michigan. Dr. Schuette noticed early flowering forms of *R. palustris* in the Green Bay region of Wisconsin. He believed them to be descendants of crosses with *R. blanda.* A collection of *R. palustris* var. *inermis* (Schuette) Erlanson from Dorset, Ontario (No. 5854), is not unusually early. On the other hand, a collection of *R. palustris* var. *aculeata* (Schuette) Erlanson from the southern shore of Saginaw Bay, Michigan (No. 5714), always begins to flower with the *R. carolina* group, considerably before any of the other plants, and is through by the time the last *R. palustris* plants are just beginning (see Table II).

This was examined cytologically and was found to have irregularities during meiosis (Erlanson, 4).

A culture grown from seed from Lebanon, New Jersey (No. 5590), is, for the most part, typical *R. palustris,* and all but one of the plants flowered on July 13–14, 1927, and on July 14–16, 1928. One plant produced a few flowers in 1927 beginning July 5; in 1928 it flowered on July 2 (see Table II). This was found to have almost completely sterile pollen in 1927 and was suspected of being a triploid hybrid. Recent cytological examination has confirmed this suspicion. The pollen parent was doubtless *R. carolina,* which species it resembles in many respects.

A dozen plants raised from seed of a hybrid *R. rugosa* × *palustris* (No. 5494) begin flowering just before the earliest *R. palustris* with No. 5714. *R. rugosa* Thunb. comes into bloom with the early diploid Cinnamomeae in mid-June.

Rosa palustris has a relatively long flowering period, three weeks or more for each plant; it does not bloom on the season's turions. The first ripe hips appear about the first of October.

Dr. Hurst (7) classifies this species as AADD; it is, however, diploid and not tetraploid.

ROSA FOLIOLOSA NUTT.

The southern diploid species *R. foliolosa* Nutt., represented by two collections from Texas and Oklahoma, begins to flower with the late *R. palustris* forms in mid-July.

Plants of *R. foliolosa* × *rugosa* sent from the U. S. Department of Agriculture (S. P. I. No. 63685), began to flower on July 5, 1928.

ROSA SETIGERA

This diploid species, belonging to the section Synstylae, comes into flower in mid-July along with *R. palustris* and *R. californica.*

ROSA RUBIGINOSA

The simultaneous production of flowers among plants of one species irrespective of their wild origin is most noticeable in *R. rubiginosa* L., a European species which has become naturalized in many parts of North America. Our garden contains plants from New York, Michigan, Arkansas, Mississippi, California and Oregon. In 1926 they all began to flower between June 21 and 24; in 1927 between June 15 and 20; and in 1928 between June 19 and 25.

APPLICATION OF PHENOLOGICAL DATA

Besides the theoretical interest in the significance of the order of flowering among the species of Rosa, the writer has found phenology to be of practical value in classifying anomalous specimens. Herbarium specimens of flowering branches are often very difficult to determine. Unarmed individuals may occur in any species, and only too often these will be named "*R. blanda*" in herbaria. Such mistakes could be avoided by noticing the date of collection, especially if one has other roses from the same region which will give some indication of the date when the various groups flower there.

Hybrid roses seem to begin flowering at some time between the flowering of the two parents. Students of the genus would find it profitable to investigate plants showing abnormal flowering time.

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THE FUNGOUS FLORA OF THE SISKIYOU MOUNTAINS IN SOUTHERN OREGON *

CALVIN H. KAUFFMAN

IN THE fall of 1925, after a lengthy stay in southwestern Washington, the writer, accompanied by his field assistant, Mr. Clair A. Brown, moved south, after the rains, to Takilma, Oregon. This village lies in a small and narrow homestead valley which pushes like a wedge into the boundary of the Siskiyou National Forest. The lower and wider end of the valley faces westward following a stream whose waters, after fifty miles of meandering, empty into the Pacific Ocean. The upper end of the valley, facing east, narrows rapidly and looking up one sees the higher peaks of the Siskiyou in the far distance. Mountain ridges flank the valley closely, and a bare half hour suffices to reach the ascending slopes of these forested ridges on either side. The valley where the scattered little homes of the prospectors and miners stand is flat grass land with scattered evergreens or open pastures. Here and there are groves of oak. The ridges, however, are composed of quite a mixture of conifers and hardwoods. Not so very far into southern Oregon from here and thence northward through Washington, *Quercus garryana* is the only oak to be seen. Here, however, probably half a dozen oaks, a variety of firs, the hemlock, the sugar pine, Libocedrus, junipers, and a large number of shrubs give sufficient variety of hosts and substrata to insure for the mycologist a rich harvest. All that is needed in addition is plenty of moisture. The coast rains had already been soaking the country for some time and when we arrived, fungi were abundant. Forest trails led southeast into the higher mountains, and within three miles of the village one found himself crossing California's northern boundary.

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* Paper from the Department of Botany of the University of Michigan, No. 307, and from the University Herbarium, No. 13.

We remained scarcely three weeks, collecting from November 25 to December 13. As the elevation in the neighborhood of the village is low — about 1500 feet — the weather was generally very mild for this time of year, and fungi of the sort whose fruiting habit may be called autumnal developed well in the showery warmer days between the periodical nights of frosts. About every third or fourth night the weather would clear and a frost of greater or less intensity would cause the more fleshy fungi to freeze. By the following noon these specimens were likely to be slightly discolored and watery, having meanwhile thawed out. In the case of the agarics, whose fruit-bodies remained in an upstanding position after thawing, and which often did not look so very different from the newly developed specimens of the same species, it was often difficult for the collector to tell which were the proper specimens to take in for study. Discrimination between species, especially of the small types, was made much more difficult. It was also discovered that specimens, of agarics especially, when dried over the heater, if they had had a touch of frost, were liable to dry as if cooked. These make poor herbarium specimens for later study. In fact, such collections often did not appear to have been frosted, even when sections were studied under the microscope, but the peculiar effect of drying often showed that they had been actually touched by frost.

One accustomed to the seasonal fruiting of such fungi in the East, or even in the Rocky Mountain area east of the Cascade Range, will find in this Pacific Coast slope, with its mild winter climate, quite a difference in the generic forms of fall and early winter as compared to those of other regions. It may be said, however, that, as a rule, the genera whose species are abundant in the autumn months in the East will be represented here also. Although an immense variety of species of Cortinarii were seen and collected in southwestern Washington during October and November on this same expedition, it is to be noted in the following list that only four species of this genus were found at Takilma. The general environment at Takilma seemed entirely appropriate for an abundance of this group, yet, strangely, they were absent.

This whole region is hardly more than touched as yet, speaking botanically, not only on the cryptogamic side, but also as regards the distribution of the flowering plants. There is no doubt that undescribed species of the latter are still waiting for the botanist.

The road west from Grant's Pass, a delightful Oregon town on the Southern Pacific Railroad just before the trains and automobiles going south begin their climb over the Siskiyou — this west-facing highway is now open to the coast and thence south on the California shore, and tourists will pass in increasing numbers through the edge of the country we were in. Its accessibility assured, its flora will doubtless soon be thoroughly studied. Up in the mountains and in fact also in the low-lying valleys of the type we visited, considerable gold has been taken out ever since the days of '49, and stories of those old days are to be heard at every turn.

In the following pages quite a number of new species of fungi from this locality have been named. In addition, a considerable number of those named by Peck and Murrill have been more fully described. The microscopic data have been especially added, since in the original description many of the genera of agarics, in which the plants are small, these characters were given either not at all or very unsatisfactorily. A proper comparison with the known European as well as eastern American species cannot be made until these facts are at hand. Twelve species in the Agaricaceae have been described as new; one in the Polyporaceae; one in the Thelephoraceae; while one of the Clavariaceae described in a former paper (12) came from Takilma. In the Ascomycetes, two Discomycetes and six Pyrenomycetes are presented as new. A number of Pyrenomycetes poorly described by Ellis in his *The North American Pyrenomycetes* from specimens sent to him by Suksdorf, the indefatigable collector of the Pacific slope region, were thoroughly revised and emended. About two hundred species of fungi were collected in this place by Mr. Brown and the writer, and most of them are listed or discussed below.

Although practically everything was collected on the Oregon side of the boundary, the flora here presented must necessarily be assumed to occur in the northern part of California as well. These records cover, of course, only a very small part of the possible fungous flora of the Siskiyou region.

Mr. Brown busied himself mostly with the wood-inhabiting fungi, while the writer collected "everything in sight." Most of the Discomycetes were identified by Dr. Bessie B. Kanouse; in the Pyrenomycetes Dr. L. E. Wehmeyer gave critical help. All material, however, has been through the hands of the author.

Papers dealing with Oregon fungi along general lines have been published as follows: Zeller (30–32), Kauffman (10) and Murrill (19–20).

ASCOMYCETES

DISCOMYCETES

GEOGLOSSACEAE

LEOTIA GELATINOSA Hill. — Under hardwoods on a slope of a ravine.

MITRULA CUCULLATA (Batsch) Fr. — On needles of *Abies sp.* Three collections.

SPATHULARIA CLAVATA (Schäff.) Rehm. — On ground among needles of Douglas fir.

HELVELLACEAE

HELVELLA CRISPA (Scop.) Fr. — Gregarious around a conifer stump. The stems of the plants in this collection are unusually long, attaining a height of 8–12 cm.

HELVELLA FAULKNERAE Copeland. — Cap irregular, hemispherical, convex in outline, agariciform rather than saddle-flapped, umbilicate, free on margin, not costate beneath, at first "fuscous black" then "hair brown" (R.), white becoming straw-colored beneath, 1–1.2 cm. high. Plant 3–4 cm. tall. Stem 6–10 (12) mm. thick, subequal, with 4–5 tubular chambers, partitions 0.5 mm. thick, continuous from top to bottom, pure white, when dried a uniform straw color, rigid and brittle, deeply fluted with edges that look like thin sharp plates when dried. Asci 270–300 × 12–16 μ. Spores ellipsoid, 16–20 × 11–14 μ, tinted a brownish pink, with one large oil drop that almost completely fills the spore, the oil drop a decided greenish tint, paraphyses straight, equal, hyaline, septate, 2–3 μ in diam.

Under needles and leaves in humus and soil at edge of road in fir and pine forest. Collected by C. H. Kauffman at Takilma, Oregon, December 8, 1925.

A collection from the Medicine Bow Mountains, Wyoming, September 12, 1923, is identical with the Oregon plant. This resembles *H. lacunosa* in some respects, but our plants of *H. Faulknerae* are very much shorter, the stem remains light-colored, the spores are distinctly tinted, the paraphyses are equal. The only Helvella that could be located with colored spores was *H. capucina* Quél., and it does not answer in other respects.

Copeland described *H. Faulknerae* from a collection made near Chico, California, but his description is so brief that a more complete one seems desirable. Seaver (28) does not recognize this plant, nor does he place it into synonymy, as he did with another species of Helvella which Copeland described in the same paper.

HELVELLA INFULA Schäff. — Gregarious on bare or subgrassy ground in an opening near a conifer forest.

The pileus is distorted and the surface is often deeply ridged-areolate, similar to the description of the pileus of *Elvela Underwoodii* Seaver: "Pileus much contorted, irregularly lobed and plicate, marked into areas by indistinct anastomosing ridges." However, the branched paraphyses with knob-like colored apices and the smooth spores agree with *Helvella infula* Schäff. (See *Physomitra infula* Boud. *Icones*, Pl. 223.) This is *Elvela infula* Schäff. per Seaver.

HELVELLA LACUNOSA Afzel. — In conifer forest.

PEZIZACEAE

OTIDEA LEPORINA (Batsch) Fkl. — Common on the ground under conifers. Same as *Scodelina leporina* (Batsch) S. F. Gray per Seaver (*l. c.*).

PEZIZA REPANDA Pers. — On ground in conifer forest. The most western point of distribution in the United States for this fungus, as given by Seaver, is Iowa. We have it also from Wyoming.

Rehm gives the substratum as decayed wood; Seaver says "occasionally on soil."

PEZIZA SYLVESTRIS (Boud.) Sacc. & Trott. — On ground.

HELOTIACEAE

CHLOROSPLENIUM AERUGINASCENS (Nyl.) Karst. — On decorticated wood of *Alnus oregona.*

HELOTIUM CITRINUM (Hedw.) Fr. — On red alder.

OMBROPHILA ENTEROCHROMA Pk. — On fallen twigs of *Libocedrus decurrens.*

PATELLARIACEAE

PATELLA CALIFORNICA Rehm. — Frequent. On decorticated saplings of Douglas fir lying on the ground and also on *Arbutus menziesii.*

The type was described from Clermont, California, from a collection made in 1910 by C. F. Baker, on dead *Adenostoma fasciculatum.*

CENANGIACEAE

BULGARIA POLYMORPHA (Flor. Dan.) Wettstein. — On tan-bark oak.

CENANGIUM LEPTOSPERMUM B. & C. — On Douglas fir. Immature.

TYMPANIS PINASTRI Tul. — On Douglas fir. Ascospores fusiform, 25–27 × 4–5 μ, greenish-hyaline; conidia innumerable.

STICTIDACEAE

OCELLARIA AUREA Tul. — On willow twigs.

OCELLARIA AUREA Tul. var. CORNICOLA Kauff. & Kanouse. — See Kauffman (13). On *Cornus sp.* This is good material and corresponds perfectly with the collection from Rock River, Lake Superior, Michigan.

PROPOLIS FAGINEA (Schrad.) Karst. — On wood of Douglas fir and *Acer circinatum.*

STICTIS MOLLIS Pers., — Rehm. — On bark of dead branch of *Umbellularia californica.*

TRYBLIDIACEAE

Tryblidium fatiscens, Kauff. sp. nov. (from *fatisco,* "to open in chinks"). — APOTHECIA loosely gregarious, at first imbedded in the wood, at length erumpent to spuriously superficial, convex, covered by the split longitudinal fibers of the wood, orbicular to subellipsoid or subfusiform in outline, sometimes with a slight papilla, opening by a pore at first or soon cracking radially and at length peeling off in places, blackish, white within, carbonaceous, 0.5–1.5 mm. in diam., 0.5 to 1 mm. high at maturity, blackening the surrounding wood surface. ASCI cylindrical, 240–270 × 15–18 μ (sp. pt. 200–240 μ), with short pedicel, 8-spored. ASCOSPORES uniseriate, elliptical, smooth, muriform, 33–36(40) × 12–15 μ, with 7–10 cross-septa, longitudinal septa rather numerous, moderately dark brown, turning blackish with iodine. PARAPHYSES slender, branched above.

On old and hard decorticated wood of *Amelanchier* (probably, *oregona*). Type collected by Clair A. Brown at Takilma, Oregon, December 2, 1925.

This species is related to *Tryblidium melaxanthum* (Fr.) Schroet. [= *Pseudographis elatina* (Ach.) Nyl.], but differs from it in its habit of developing in the woody tissue instead of the bark, by occurring on hardwoods instead of conifers, by its larger spores with greater number of cross-septa, and by the more rounded and protuberant perithecia-like apothecia; some apothecia have a tendency to form an indistinct papilla where the dehiscence is initiated; others may show an initial longitudinal crack, especially when elongated. From *T. calyciforme* Rebent. it differs by its cylindric and larger asci and the mostly hemispherical-convex apothecia. The ascospores of *T. carestiae* (De Not.) Rehm have hyaline appendages and differ otherwise. Its mode of pushing up the surface fibers of the wood is similar to that in the account of Ellis for his American specimens of *Pseudographis elatina.* There is no sign of a gelatinous envelope to the spores. The ascospores are intensely stained by iodine, a characteristic of the genera Pseudographis and Tryblidium, according to Rehm (*Discomyc.*, p. 99).

PHACIDIACEAE

CLITHRIS MORBIDA (Pk.) Ellis. — On decorticated wood of *Pseudotsuga mucronata.* Although the material is somewhat immature, it shows much to indicate that this is its place.

GLONIUM TRYBLIDIOIDES E. & E. — On old decorticated wood of *Pseudotsuga mucronata.*

Hysterographium Arctostaphyli Kauff., sp. nov. — PERITHECIA scattered-gregarious, superficial, ellipsoid or elongated ellipsoid, 1–1.5 mm. or less in length, 0.5 mm. wide, rounded at ends, black, dull, slit reaching to both ends and at length gaping, even or indistinctly striate. ASCI subcylindric, sp. pt. about 120 × 25–30 μ. ASCOSPORES ellipsoid or slightly narrowed toward ends, scarcely or not at all constricted, one section above middle swollen at maturity, the two halves somewhat unsymmetric, obtusely rounded at ends, with 7–9 (rarely 11) cross-septa, dark brown, 40–52 × 14–16 μ.

On decorticated old wood of *Arctostaphylus columbiana.* Type collected by Clair A. Brown, at Takilma, Oregon, December 6, 1925.

This species differs from *H. vulvatum* (Schw.) Sacc. to which it seems related, by the much fewer cross-septa and other differences in the spores, as well as in the surface marking of the perithecia.

HYSTEROGRAPHIUM FRAXINI (Pers.) De Not. — On bark of dead branchlets of *Fraxinus oregona.* The large elliptical spores are not at all constricted, although authors say they are slightly so.

HYSTEROGRAPHIUM PROMINENS (P. & H.) Berl. & Vogl. — On old decorticated wood of *Arctostaphylus columbiana* (the manzanita bush). The ascospores of this species are markedly different in shape and structure from those of *H. Arctostaphyli* described above; those of the former are fusiform, constricted sharply, long and narrow, while those of the latter species are shorter, obese; the region above the non-constricted middle is often swollen and there are fewer cross-septa. *H. Nova-cesariense* Ell. has smaller perithecia than either of these, and the longitudinal septa of its spores are few, while in both of the species on manzanita the longitudinal walls are numerous and well marked. The spores of *H. prominens* fall easily into two parts at the constriction.

PYRENOMYCETES

HYPROCREACEAE

HYPOCREA PALLIDA E. & E. — On pore surface of a fruit-body of *Fomes pinicola.*

NECTRIA CINNABARINA Fr. — On dead twigs of an Amelanchier and of cultivated apple tree; on the latter it was mostly in the Tubercularia stage.

NECTRIA EPISPHAERIA (Tode) Fr. — On stroma of *Diatrype stigma.*

NECTRIA SP. — On dead branches of Philadelphus. In the present state of the literature on this group, it seems unwise to name and describe this. The perithecia are crowded in small clusters on small salmon-pink stromata (1 mm. or less in diameter), dark red, becoming darker, roughish, and the ascospores measure 19–25 (28) × 5.5–7 μ. The stromata and perithecia push through the bark. The large ascospores suggest *Nectria diploa* B. & C. given by Seaver (*l. c.*) under Creonectria, but they are not as broad, and the perithecia are not "bright red."

DOTHIDIACEAE

PLOWRIGHTIA MORBOSA (Schw.) Sacc. — On *Prunus sp.*

SPHAERIACEAE

BERTIA MORIFORMIS (Tode) De Not. — Frequent. On old decorticated wood of *Acer macrophyllum,* of *Alnus oregona* and of *Libocedrus decurrens.*

HERPOTHRICHIA NIGRA Hartig (?). — Forming extensive sooty patches on standing trunks and branches of *Pseudotsuga mucronata.* This material was sterile and it may of course be *Neopeckia Coulteri* (Pk.) Sacc. Its habit on bark is unusual, but in its structure and otherwise it seems to belong here.

MELANOMMA PARASITICA E. & E. — On the stromata of *Diatrype stigma.*

ROSELLINIA LIGNIARIA (Grev.) Sacc. — On decorticated wood of *Acer macrophyllum* and *Sambucus callicarpa.* The species here so referred is notable by the bleached whitish areas surrounding the patches of perithecia. The perithecia are black, densely hairy-hirsute nearly up to 0.3 mm. in diam. The asci measure 75–85 (sp. pt.) × 8–9 (10) μ. The ascospores are elliptical, smooth, fuscous, rounded-obtuse at the ends, measuring 12–14 (15) × 7.5–8.5 (9) μ. Harkness' species, *R. rynchospora,* is described with spores that are provided with curved brown appendages at each end, and the spores are larger.

ROSELLINIA LIGNIARIA forma PINI Sacc. — On old decorticated wood of *Pinus ponderosa.* This differs from the typical species not only in its coniferous host, but also in the size of the ascospores, which measure 14–17 (18) × 8.5–10.5 (12) μ and are dark brown with an indistinct purplish tint. Ellis described a species from Seattle, on pine, as *R. pulcherrima* E. & E., but this has appendages and much narrower spores. Many forms of *R. ligniaria* have been named. Some of these, like the one here discussed, are doubtless good species.

ROSELLINIA PULVERACEA (Ehr.) Fck. var. MILLEGRANA (Schw.) Ellis. — On decorticated oak.

CUCURBITARIACEAE

CUCURBITARIA BERBERIDIS (Pers.) Gray. — On *Berberis sp.*

LOPHIOSTOMATACEAE

Lophiostoma submagnum Kauff. sp. nov. — PERITHECIA scattered, seated in the woody tissue at the base, becoming exposed by the peeling away of the old bark, oval, black, wall thick, carbonaceous, 350 to 500 μ in cross-section, about 1 mm. high (inclusive of neck), surface roughish-granulate, with dull luster, neck stout, compressed, almost half the diameter of the perithecia, with a prominent slit-like ostiole. ASCI clavate, rounded-obtuse at apex, 8-spored, 90–100 × 10–12 μ, with abundant filiform paraphyses; ASCOSPORES fusiform, 5–7-septate, olive-brown, straight or slightly curved, 22–30 × 6–7 μ, the mature spores slightly constricted at septa.

On old dead stems of *Philadelphus gordonianus*. Type collected by Clair A. Brown at Takilma, Oregon, December 7, 1925.

Differs from *L. macrostomoides* Ces. & De Not. by its smaller asci and spores, fewer septa in the spore and by its host relations. *L. pseudomacrostomum* Sacc. has stouter spores, according to the description. The perithecia of our plant are much larger than in *L. caulium* (Fr.) De Not., the diameter sometimes reaching to 1 mm.

MASSARIACEAE

MASSARIA PUPULA (Fr.) Tul. — On bark of dead branches of *Corylus californica*. The outstanding character of this species is the peculiar constriction of the gelatinous envelope of the ascospores; this constriction extends entirely to the spore at its middle. The ascospores are 3-septate, one of the cells next to an end cell is swollen, and they measure 45–50 (52) × (14) 19–21 μ, being ellipsoid, rounded at ends and dark olive brown. The asci are large, oval, about 100 × 36 μ, associated with abundant filiform paraphyses. The perithecia are somewhat smaller than the size given by Winter (Rabenhorst, Vol. 2), but otherwise the same.

VALSACEAE

DIAPORTHE DECEDENS (Fr.) Fkl. — On bark of dead branches of *Umbellularia californica* (Oregon myrtle) and of *Corylus californica.*

ENDOXYLA OPERCULATA (A. & S.) Fkl. var. **compressispora,** Kauff. var. nov. — On old decorticated wood of *Pinus ponderosa.*

This has the characters of *E. operculata* except for the compressed spores, which, however, is a marked difference. There is no black stromatic line present around the loosely grouped perithecia. The surface of the wood is extensively bleached. The perithecia are black, 0.5 to 0.7 mm. in diam., easily falling out of the scarcely changed wood, with large, open, pezizoid, flaring ostioles on stout necks. The ascospores are brown, elongated-oblong, straight, continuous, compressed in one longitudinal plane, and measure 10–13 × 3–4 μ, the ends rounded or faintly subtruncate. The asci were mostly overmature.

Type collected by Clair A. Brown at Takilma, Oregon, December 2, 1925.

E. lineata Cke., also on pine, is said to have allantoid spores. It differs from *E. parallela* by its compressed non-septate spores, which would readily be found in material as mature as this. Our material covered a considerable surface of an old decorticated sapling trunk lying on the ground.

ENDOXYLA PARALLELA (Fr.) Fkl. — On decorticated wood of *Pinus ponderosa*. Two collections were made of this. The typical, clavate asci measure 50–60 (sp. pt.) × 7–8 μ, are stipitate and with biseriate, brown, oblong, obtuse, 1–2-septate, straight ascospores, which measure 13–15 × 3–4 μ. Mixed with the perithecia are very similar perithecia containing different asci and spores. These two types of perithecia are associated in the same clusters. The asci of the second type are longer, cylindrical, 60–65 (sp. pt.) × 4 μ, and the ascospores are much shorter, oblong, uniseptate, brown and measure only 5–7 × 2.5–2.75 μ. Asci of both have rather long pedicels. The perithecia are all about equally mature, and septa are to be seen in abundance in the spore-containing asci of both types. In the one, the single septum is entirely constant. In the other the uniseptate and biseptate spores are both in evidence and occasionally one can find a spore with three septa. Whether two distinct fungi are concerned could not be determined. In these species of Endoxyla the stroma is said to be lacking, but doubtless slight stromatic areas are present in the neighborhood of the loosely grouped or scattered perithecia.

EUTYPA FLAVOVIRENS (Fr.) Tul. — This is a common species in this region. It was found on decorticated wood of *Ceonothus cuneatus*, *Populus trichocarpa*, *Acer macrophyllum*, *Acer circinatum* and *Quercus sp.* The ascospores of American plants are not given by Ellis (7); they are allantoid, subhyaline, i.e., slightly tinged brown, 6–8 (9) × 1.5–2 μ. The perithecia are about 0.25 mm. or less in diam. This species and the following one are reported by Zeller (31).

EUTYPA LATA (Pers.) Tul. — On old decorticated wood of Quercus. The asci are 55–60 μ long (sp. pt. 36–48 μ) × 5–6 μ wide, 8-spored. The ascospores are allantoid, subhyaline or tinged with brown, obtuse, 10–12 × 2.5–3 μ. Except for the slightly thicker spores, this collection fits well into the species given.

EUTYPELLA CERVICULATA (Fr.) Sacc. — A form of this composite group of forms was collected on *Alnus oregona*. Another form on Corylus.

EUTYPELLA MINUTA Berl. & Sacc. — On dead bark of *Umbellularia californica*. The ascospores are allantoid, yellowish-hyaline and measure 7–11 × 2.5–3 μ. Identified by L. E. Wehmeyer.

Eutypella oregonensis Wehmeyer, sp. nov. — STROMATA scattered, sometimes confluent, strongly pulvinate to hemispherical, 0.8–1.5 mm. in diam.; periderm closely adherent, overarching the stroma at first, becoming laciniately ruptured and exposing the blackened disk with its few small, hemispherical and sulcate ostioles. PERITHECIA spherical to flask-shaped, 300–420 × 300–600 μ, varying in number, 2–8 (10) in group, partially imbedded in the white ectostromatic substance. ASCI long-clavate, with a long stipitate base, 75–85 × 7–9 μ, pedicel 25–40 μ in length. SPORES allantoid, 1-celled, biseriate, yellowish-brown, 9–14 (16) × 2–3 (3.5) μ.

Type collected by Clair A. Brown, on dead branches of *Acer sp.*, at Takilma, Oregon, December 10, 1925.

Although the ectostromatic portions are prominent, the entostromatic portion bears the perithecia and is more or less continuous below throughout the bark, with blackened zones which are irregularly scattered and not very definite. Its strongly developed stromatic disk is rather characteristic and makes it appear somewhat like a Diatrype, but the closely adherent periderm and conical shape of the pustules place it in Eutypella.

RHYNCHOSTOMA TINCTUM (E. & E.) Sacc. — On decorticated wood of oak and of *Acer macrophyllum.* The perithecia are finally superficial, black, about 200–250 μ in diam., with moderately slender necks 300 to 600 μ long. The asci are clavate, tapering to the short pedicel, 30–40 × 6–7 μ (sp. pt. 20–24 μ), 8-spored. Ascospores subfusiform or elliptical-subventricose, brown, 2-celled, 7–9 × 2.5–3 μ. Paraphyses numerous, filiform, equal. The size of the spores as given by Ellis (7) is a little too small, but this is without doubt his species and was described on the large-leaved maple from Washington.

VALSA SALICINA (Pers.) Fr. — On bark of a species of Salix.

DIATRYPACEAE

CALOSPHAERIA PULCHELLOIDEA (Cke. & Ell.) Ellis. — On decorticated oak wood. "This seems to be identical with Ellis' type specimens, distributed as No. 496 (*N. A. F.*). It differs from it in the crowding of the perithecia into dense clusters on the decorticated wood surface and in the generally shorter necks, but these are probably variable characters. When placed in water, the tips of the asci gelatinize and swell out into thin-walled vescicles. The thickened walls just behind the apex constrict and squeeze the spore-mass into this vescicle which eventually bursts and frees the spores." This study was made by L. E. Wehmeyer.

Ellis, in *The North American Pyrenomycetes,* says the perithecia are seated on the surface of the inner bark, with long, slender, but very brittle ostioles, erumpent through the epidermis but not united into a disk. In our specimens the bark has disappeared thoroughly and the perithecia are almost superficial on the wood. This different habit is, however, not impossible and the perithecia may have been initiated under the bark and developed slowly. In the absence of bark, the necks have remained shorter and their brittleness is apparent. The perithecia are arranged in rows or narrow strips, as described by Ellis. The collection was made December 1.

Diatrype diffindens Kauff., sp. nov. — STROMATA at first immersed in the wood, pushing through the surface as lentil-shaped or fusiform humps, 1–2 mm. × 0.5–0.75 mm., then splitting the wood fibers longitudinally, only the surface becoming exposed at maturity, with a faint dark zone separating them from the wood. PERITHECIA 0.25–0.33 mm. in diam., oval, 2 to 6 or rarely more in a stroma, loosely arranged, the ostioles quadrisulcate or stellate and enlarged, the necks short and emerging separately. ASCI clavate on long slender pedicels, 8-spored, 60–70 × 6–8 μ (sp. pt. 32–38 μ). ASCOSPORES allantoid, subhyaline, tinged brownish, obtuse, somewhat curved, 9–11 (12) × 2.5 (3) μ.

On decorticated twigs of fallen dead saplings of *Pseudotsuga mucronata.* Type collected by Clair A. Brown at Takilma, Oregon, December 9, 1925.

This species seems to approach *D. microstega* E. & E. from California; host unknown. Our plant, however, has smaller perithecia and stouter ascospores; the stromata are in the wood instead of the bark, do not become superficial, and are larger and often elongated. Species of this genus are rarely reported on coniferous wood. The separately erumpent ostioles bar it from the genus Eutypella and the stellate ostioles from the true Valsae. The well-developed, even if immersed, stroma with the darker limiting zone indicates its position here.

DIATRYPE MACOUNII E. & E. — This is common in the region covered, mostly on species of oak and willow. It was originally described from material sent to Ellis from British Columbia on maple. It is evidently widely distributed in the Pacific states of the Northwest. The stromata are rather small but numerous and distinct, sometimes approaching in size and appearance those of *D. bullata* (Hoff.) Fr. It must be carefully distinguished from *D. disciformis* of Europe (Hoff.) Fr., which has larger spores. Whether Ellis' own var. *americana* of this latter species is really referable to *D. Macounii* remains to be seen. Our plants have consistently small ascospores, by which they are readily distinguished from species whose stromata have a similar appearance. The asci are 8-spored, but in the overmature condition the species might well be confused with *Diatrypella discoidea* Cke. & Pk., as its spores are very similar in size and other respects to the latter. The very long and slender pedicels of the asci terminate in the short clavate-subfusiform spore-bearing portion which measures only about 15–20 × 3 μ. The ascospores are allantoid, tinged yellowish-brown, minute, 5–6 × 0.8–1 μ. Ellis' description is quite complete.

DIATRYPE PROMINENS Cke. & Hark. — On decorticated hard wood of *Umbellularia californica* and *Quercus garryana.* It is probably common. This has a striking stroma when fully developed. Ellis seems to have been confused about this species (7) and did not find spores of the size reported by Cooke, viz. 12–13 × 2 μ. With the excellent material on hand it is possible to give somewhat more exact data.

STROMATA vary in shape, orbicular to ellipsoid or oblong, or somewhat hemispherical, often forming narrow long strips by confluence, black, 1–2.5 mm. when rounded, 2–3 × 1 mm. when elongated, confluent strips from 4 to 12 mm. long, about 1 mm. high, cinerescens inside, entirely denuded in age. PERITHECIA crowded in the lower part of the stroma, ellipsoid, often compressed, about 0.5 mm. high, the prominently protruding necks rather stout, separately erumpent and with large stellate or quadrisulcate ostioles. ASCI clavate-subfusiform in the spore-bearing part, pedicellate, 60–80 × 5–7 μ (sp. pt. 35–40 μ), 8-spored. ASCOSPORES allantoid, obtuse, subhyaline, sometimes only slightly curved, 9–12 × 2–2.5 μ.

DIATRYPE STIGMA (Hoff.) Fr. — On fallen oak and willow branches.

Diatrype stigmaoides Kauff., sp. nov. — STROMATA forming under the periderm which is soon thrown off, i.e., widely erumpent, widely effused, continuous or interrupted, 2–10 cm. or more long, 1–4 cm. or more wide, 0.5–1 mm. thick, whitish within and with a greenish tint in age, surface grayish-black with a slight resinous luster, with a rich development of the entostromatic tissue above the perithecia, *without entostromatic columns extending into the lower bark* as they do in *D. stigma*, margin thick and determinate. PERITHECIA oval, black, immersed in stroma, *neck long and slender*, with rather large, quadrisulcate separately projecting ostioles, about 0.5 mm. in diam. (480–540 × 400–450 μ), monostichous or sometimes subsuperposed. ASCI 8-spored, slender, long-stalked, 125 × 5–6 μ (sp. pt. 20–25 × 5–5.5 μ). ASCOSPORES *minute*, subhyaline with yellowish tint, very narrow, allantoid, 4–5.5 (6) × 0.5–0.8 (1) μ.

Type collected by Clair A. Brown, on fallen white oak branches, at Takilma, Oregon, December 6, 1925.

The general similarity of this species to the common *Diatrype stigma* makes it easy to pass it by. When, however, the surfaces of the stromata of the species are compared under a magnification of 25 diameters, the differences stand out markedly. In the new species the ostioles are then shown to be prominently exserted and quadrisulcate and the shallow circular depression around the ostiole, which is seen in *D. stigma*, is nearly lacking. The surface is less even and cracks more extensively into blocks, and the luster is different. Microscopically the spores are much smaller than in *D. stigma*, where they normally measure 7–9 × 1.5 (2) μ.

DIATRYPELLA DECIPIENS E. & E. — On dead corticated branches of *Corylus oregona*. The stromata have very much the appearance of *Diatrype bullata*, but the asci are polyspored. The ascospores are minute and measure 4–5 × 0.5–0.8 μ, allantoid and hyaline.

DIATRYPELLA DISCOIDEA Cke. & Pk. var. ALNI Pk. — Frequent on dead branches of *Alnus oregona*.

XYLARIACEAE

HYPOXYLON COHAERENS Fr. — On bark of dead branches of *Corylus oregona*. As stated elsewhere (13), Ellis (7) gives the size of the spore-bearing part of the ascus erroneously. Asci (sp. pt.) 70–85 × 6–7 μ, cylindrical, 8-spored. Ascospores uniseriate, elliptical, subventricose, dark brown, 10–12 × 4.5–5.5 μ.

HYPOXYLON FUSCOPURPUREUM (Schw.) Berk. — On *Umbellularia californica, Amelanchier sp.* and *Quercus sp.* An emended description appears elsewhere (13).

HYPOXYLON MALLEOLUM B. & Rav. — On rotten wood of oak. This is in reality a Daldinia. I first collected it in Florida and later studied the specimens in the Ravenel collections at Washington, D.C. Its known distribution starts in the Carolinas on the eastern seaboard, then southward, probably extending along the Gulf States and into the tropics, and appearing again in the southwestern United States where it has now been shown to occur as far north as southern Oregon. Ellis (7) has given a revised although incomplete description.

STROMATA vary from convex-pulvinate to globose, ranging in size from 1 cm. to 2.5 cm., sometimes composite by their confluence, sometimes broadly sessile, sometimes slightly narrower at base, black, ornamented on the surface by separated, shallow craters, 0.5 to 0.7 mm. across, in the center of which is the slightly projecting obtuse papilla, surface has a somewhat resinous luster, black, concentrically zonate and shining within. PERITHECIA peripheral, oval to ellipsoid in outline, 1 mm. × 0.7 mm., imbedded in a differentiated separable outer layer about 1 .25 mm. thick, with a perithecial wall of their own. ASCI long and slender, cylindrical, 180–190 × 5–6 μ (sp. pt. 135–140 μ), 8-spored, with a slender pedicel about 40 μ long, soon evanescent, at least when mounted in water. ASCOSPORES uniseriate, subfusiform, almost straight, brownish (later dark brown), somewhat unsymmetric, ends subobtuse, 18–22 × 4–5.5 μ.

Apparently it occurs mostly on oak, although also reported on poplar. Since the concentric structure and the larger size of the stromata are the main distinction between Hypoxylon and Daldinia, this species should be called **Daldinia malleola** (B. & Rav.), comb. nov.

Hypoxylon oregonense Kauff., sp. nov. — Stromata superficial, 0.5–0.66 mm. thick, forming determinate elongated strips, varying 1–4 (up to 10) cm. long, sometimes confluent and longer, 0.5–1 cm. wide, margin at first thin and effused, determinate and fertile at maturity, "maroon" (R.) color to "diamine-brown," concolorous within at first, becoming darker to blackish in age, especially inside; surface marked by slightly raised, low, convex areas in the center of which minute white pores appear, at length rimose to subareolate between the perithecial units, minutely subtomentose to pulverulent, with a dull luster. Perithecia monostichous, oval to narrowly elliptical, about 350–400 μ long × 200 μ wide, immersed in the stroma, provided with abruptly slender necks which reach the surface of the stroma but do not project, terminated at maturity by the whitish ostiole. Asci cylindrical, 8-spored, with long and slender pedicel, paraphysate, 150–160 × 7–9 (11) μ (sp. pt. about 100 μ long). Ascospores subventricose-ellipsoid (one view), convex-plane (other view), obtuse to subacute at ends, dark brown or with tint of purplish, 14–18 (19) × 6–7 (8) μ.

On old decorticated wood of *Quercus sp.*, *Amelanchier florida* and *Arbutus Menziesii* (Madroña tree). Type collected by Clair A. Brown at Takilma, Oregon, December 2, 1925, on *Amelanchier florida.*

By the large spores and asci alone this species can be easily distinguished from other species having a similar purplish stroma, as, for example, *H. atropurpureum* Fr.–Winter and *H. fuscopurpureum* (Schw.) Berk. Four collections were made, any of which could have served as the type material. The surface of the wood is blackened only slightly or not at all in the vicinity of the stroma.

Hypoxylon pruinatoides Kauff., sp. nov. — Stromata superficial, flattened-convex and somewhat tubercular, gregarious to confluent, elliptical or irregular in shape, 3–6 mm. by about 3 mm. wide, at first covered by a vinaceous-grayish conidial pubescence, later subfuscous, umber to blackish within. Perithecia monostichous, crowded, narrowly elliptical, lying in the upper portion of the stroma, about 400 × 200 μ in size, with very short necks which open by minute, whitish, non-projecting ostioles. ASCI cylindrical, (sp. pt.) about 70–80 × 6–7 μ, with a long slender pedicel. ASCOSPORES ellipsoid (one view, convex-plane other view), obtuse at ends, dark brown, 12–14 × 5–6 μ.

On the bark of a fallen branch of *Corylus californica.* Type collected by Clair A. Brown at Takilma, Oregon, December 12, 1925.

The stromata at certain stages have somewhat the appearance of the well-known *H. pruinatum* (Kl.) Cke. on poplar, but the ascospores are markedly smaller than those of the poplar fungus. The remarks of Ellis (7) on *H. janthinum* Cke. and his description of the latter species are suggestive of ours, but Cooke's species is said to have a thin and much smaller stroma, the perithecia are said to lie low, to penetrate the wood, and the spores are longer and narrower.

HYPOXYLON SERPENS (Pers.) Fr. — On rotten decorticated wood of *Arbutus Menziesii.* The collection referred to this species, rather poorly understood in this country, agrees very well indeed with the description given by Winter (Rabenhorst, Vol. 2). I have found it only rarely, owing, perhaps, to the rotten condition of the wood where it occurs and also to the small numbers of the stromata usually formed. The stroma forms narrow elongated strips, its surface being rendered uneven by the projecting convexities of the perithecia. The ascospores measure 12–15 × 4.5–5.5 μ, and are, therefore, a bit smaller than those of European material.

NUMMULARIA BULLIARDII Tul. — On *Quercus sp.*

FUNGI IMPERFECTI

HISTIOMYCETES von Höhnel

MELANCONIELLA DECORAENSIS Ell. — On bark of Corylus. Associated with *Massaria pupula.*

SPORONEMA STROBILINUM Desm. — On fallen cones of *Libocedrus decurrens.*

CYTOSPORA MICROSTOMA Sacc. var. AMELANCHIERIS Cke. — On *Amelanchier flavida.*

SCLEROPHOMA PITHYOPHILA (Corda) v. Höhnel. — Common. On needles of western yellow pine and of *Libocedrus decurrens.*

HYPHOMYCETES

TRICHOSPORIUM UMBRINUM (Pers.) Lind. — This is the conidial stage of a Hypoxylon. On old wood, probably of oak.

SIRODESMIUM GRANULOSUM De Not. — On poplar wood.

TORULA CONGLUTINATA Corda — On old weathered and whitened logs of *Pseudotsuga mucronata* and *Abies grandis.*

BASIDIOMYCETES

PROTOBASIDIOMYCETES

TREMELLACEAE

EXIDIA GLANDULOSA Fr. — On dead oak branches.

EXIDIA UMBRINELLA Bres. — On sticks of Salix and Amelanchier.

GRYOCEPHALA RUFA (Jacq.) Bref. — On needles and rotten wood, under fir and cedar.

TREMELLODON GELATINOSUM Fr. — On wood remains, sprayed by running water.

TREMELLA MESENTERICA Fr. — On oak wood.

TREMELLA FOLIOSA Fr. — On oak wood.

DACRYOMYCETACEAE

CALOCERA "CORNEA Fr." — On old oak wood. This has the habit and appearance of the species, but the spores are too long; they measure 9–12 × 3.5–4.5 μ.

DACRYOMYCES PALMATA (Schw.) Burt. — This is the same as *Dacryopsis palmata* (Schw.) Lloyd; it is also apparently *Dacryomyces chrysosperma* B. & C.

AUTOBASIDIOMYCETES

THELEPHORACEAE

CONIOPHORA LAETICOLOR Karst. — On rotten wood of western yellow pine.

CORTICIUM LIVIDO-CAERULEUM Karst. — On decorticated poles of Douglas fir lying on the ground. See remarks by Kauffman (13).

Craterellus cristatus Kauff., sp. nov. (see Text Fig. 3). — FRUCTIFICATION fleshy, 1–2.5 cm. high, suberect or erect, narrowly cornucopia-shaped, 2–5 mm. wide at apex, tapering equally downward to the slender, curved, inserted base, truncate-flattened or subconcave at top, "vinaceous buff"(R.) and glabrous throughout, solid and paler within; margin of top at first entire, then becoming cristate with prolongations which are flat, slender, 0.5–0.75 mm. wide, varying from 1 to 2 (6) mm. high, 5 to 10 in number, and forming a fringe on the margin of the flat top. HYMENIUM both covers the flattened top and extends downward exteriorly to within about 5 mm. of the base, even, not ridged nor noticeably different in color or texture from the base of stem portion which is inserted in the wood by the naked or very slightly hairy base. SPORES minute, subcylindric, hyaline, 4–5 (6) × 2–2.3 μ; cystidia none; basidia 65–70 × 4 μ, slender, 4-spored; hymenium also provided with slightly darker cells, 3–5 μ in diam., having the appearance of lactiferes, extending deep into subhymenium. ODOR none.

Type collected by C. H. Kauffman, on partly decayed logs of Douglas fir, at Takilma, Oregon, December 5, 1925.

The small size, the development of the cristate margin, the even hymenium, color and spores, separate this from its allies. In its largest development the prolongations become thicker and longer than the ordinary average, and show a tendency to a second cristation at their apices, but this is rarely seen even in rather numerous collections. The fructifications develop slowly and often they are found without the fringed top, especially early in the rainy season. They are fleshy in texture or at most slightly toughish and dry to a dark fuscous color.

HYPOCHNUS RUBIGINOSUS Bres. — On bark of oak.

HYPOCHNUS SPONGIOSUS (Schw.) Burt. — On rotten coniferous wood.

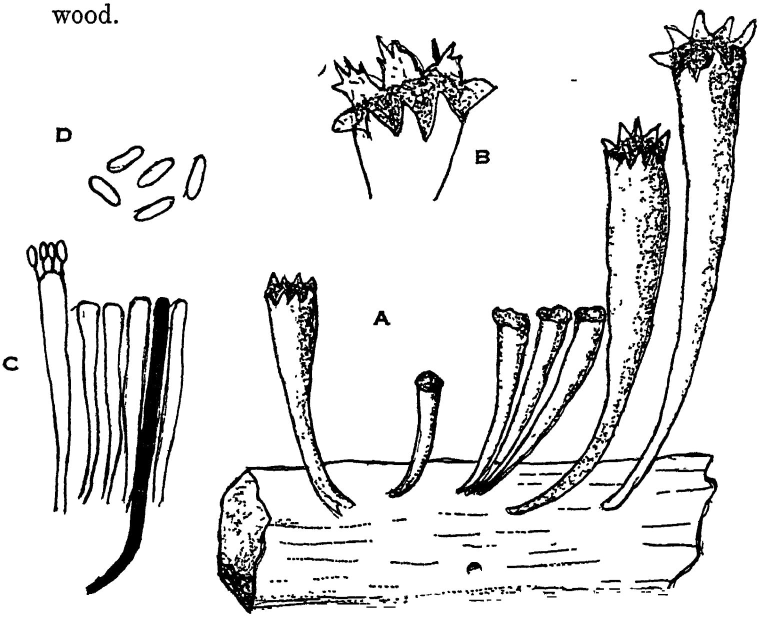

FIG. 3. CRATERELLUS CRISTATUS Kauff., sp. nov. *a*, natural size of fructifications showing habit; *b*, showing double cristation; *c*, hymenium with basidium and lactifere-like hypha, which is shown too dark; *d*, spores

PENIOPHORA CRASSA Burt. — On decorticated log of western yellow pine.

PENIOPHORA GIGANTEA (Fr.) Massee. — On decorticated wood of western yellow pine.

PENIOPHORA MINIATA (Berk.) Burt. — On decayed coniferous wood.

PENIOPHORA PUBERA (Fr.) Sacc. — On oak wood.

PENIOPHORA TEXANA Burt. — On decorticated rotten log of Libocedrus. Our plant agrees with this species in all respects except that the hymenial surface is not cracked.

STEREUM FASCIATUM Schw. — On dead wood of "live oak" and other oaks.

STEREUM HIRSUTUM Fr. — On dead alder twigs.

STEREUM PURPUREUM Fr. — On wood of Madroña and on old sticks of oak.

STEREUM SANGUINOLENTUM Fr. — On bark of a dead sapling of Douglas fir.

THELEPHORA CARYOPHYLLEA Fr. — On the ground under Libocedrus.

SOLENIA ANOMALA (Pers.) Fkl. — On bark of dead branch of *Umbellularia californica*.

HYDNACEAE

HYDNUM AURISCALPIUM Fr. — On cones of Douglas fir.

HYDNUM ERINACEUS Fr. — On living trunks of *Quercus garryana*, about 6 feet from the ground.

"HYDNUM" HIMANTIUM Schw. — This species is of wide distribution in the northern part of the Northern Hemisphere. It is one of the old *resupinate group* of hydna. Bourdot and Galzin (4) have placed it in the Clavariaceae as *Ceratella himantia* (Schw.); Killermann (14), in the new edition of Engler and Prantl, follows Bresadola (2) and gives it as *Odòntia himantia* (Schw.) Bres. It does not seem to occur in Great Britain, since Rea (24) omits it. In the United States it develops in the late fall, winter or early spring from the Atlantic to the Pacific Coast. It occurs on old, rotten frondose or coniferous wood, on the near under side of moist logs, on sticks, acorns, and the like, especially of oak. On the latter substratum it has been best known as *Hydnum subfuscum* Pk., which appears to be a synonym of it. The mycelial cords are not always present, but are frequently seen when the plant is forming on acorns and trash underneath a bed of leaves in the woods, and is often sterile under these conditions. The time seems to have come when the resupinate hydna should be removed from the genus Hydnum, as most authors are doing, but it is not clear to me why this should not be placed in the genus Acia Karst. except that the subiculum is not truly waxy. There is, however, a waxy feel to the otherwise soft and floccose substance when it is moistened and I think this is the logical place for it. As a good description does not seem available to American students I append one taken from a study of the Takilma material.

FRUCTIFICATION resupinate. SUBICULUM adnate to subseparable, effused, thin, soft, floccose-submembranous, white and sterile for some time, the thicker portions at length producing loosely disposed aculeae and changing to "cartridge-buff" (R.) or "pinkish-buff," fertile portions 1.5–2 mm. thick becoming guttulate-spotted; context floccose, the hyphae about 2 μ in diam., thick-walled with narrow lumen, hyaline, smooth, septa with clamp connections. ACULEAE scattered or in loose groups, sometimes in groups of 2–3, coherent at base, slender, narrowly conical and pointed, entire, whitish to pinkish-buff, 1.5–2.5 mm. high. SPORES cylindrical, hyaline, smooth or indistinctly granulose, obtuse, 8–12(14) × 3–4.5 μ; cystidia none; short cystidioles, scarcely extending above hymenium, are sometimes seen; basidia simple, 4-spored, about 30 × 6–7 μ; sterigmata slender, 6–7 μ long.

Collected on old bark and wood of arbutus (Madroña) and on coniferous wood.

The spore size varies, depending on maturity, and if one examines an insufficient amount of material, spores, both attached and loose, may be found, which are only 8–10 μ long. In good material, however, there is quite a percentage above 10, often 12 and 14 μ long. Bourdot and Galazin (*l. c.*) give them 7.5–10(12) × 4–5 μ.

HYDNUM IMBRICATUM Fr. — Under sugar pine and oak.

HYDNUM REPANDUM Fr. — Only a small slender-stemmed specimen was found. The color, fleshy consistency and spores are the same as those of this well-known species, but in its habit and the spaced aculeae it is aberrant. Under oak and sugar pine.

HYDNUM SUAVEOLENS Fr. — Under oak and sugar pine.

ODONTIA FIMBRIATA Fr. — On *Umbellularia californica.* Now separated from Odontia because of the presence of cystidia and placed by authors in Patouillard's genus Mycoleptodon. From coast to coast.

ODONTIA SUBOCHRACEA Bres. — On Umbellularia also.

RADULUM OWENSII Lloyd. — On oak and alder wood. This is easily mistaken for an Irpex. The spores are hyaline, oblong, obtuse, smooth, 5.5–7.5 × 3–3.5 μ. True cystidia are lacking, but short "cystidioles" can be found. The plants vary from "antimony yellow" when young to rusty orange at maturity, becoming still darker when dried.

CLAVARIACEAE

CLAVARIA CONJUNCTA Pk. — On humus in conifer forest. Spores 9–12 × 3.5–4 μ, subcylindric, minutely rough, subhyaline with a yellowish tint under the microscope. Cystidia none. Basidia 8–8.5 × 5–6 μ, 4-spored. Fructifications 10–15 (20) cm. high, with quite a number of main branches on the simple stem which is usually imbedded in humus, "cream color" to "Naples yellow" (R.), deeper upward, apices of terminal branchlets pinkish-yellow, soon yellow; rather fragile. Coker (6) makes this a synonym of *C. botrytis* (Pers.), which appears to me an untenable action. As Peck (22) has pointed out, it reminds one of *C. flava* Fr. and is related to that species. As is often true of color in mushrooms, the young or quickly developed but still entirely fresh plants of this species, *in situ*, have on the upper extremities a flesh or reddish tint which soon disappears, and so the apices appear yellow.

CLAVARIA CRISTATA Fr. — Growing on fir needles.

CLAVARIA JUNCEA Fr. — Growing in very moist and partially decayed oak leaf beds.

CLAVARIA MARICOLA Kauff. (*Pap. Mich. Acad. Sci., Arts and Letters,* 8: 149. 1927). — On needle beds of western yellow pine, attached to fallen male cones and to needles.

CLAVARIA PISTILLARIS Fr. forma TRUNCATA Atk. — Under conifers.

CLAVARIA SUBBOTRYTIS Coker (see *Pap. Mich. Acad. Sci., Arts and Letters,* 8: 150, 1927, for discussion by Kauffman). — On humus, under conifers.

POLYPORACEAE

MERULIEAE

MERULIUS NIVEUS Fr. — On dead alder branches and trunks, often intergrown and mixed with mosses. This is the only host given by Burt (5). At Lake Quiniault, Washington, it was also found on poplar. This species is known also as *Trogia Alni* Pk., *Plicatura Alni* Pk. and *Plicatura nivea* (Fr.) Karst. Its presence in Oregon has recently been reported by Zeller (32).

Its development was observed during several weeks, under conditions most favorable for its growth. The whole fructification when growing is pure snow white. In the fresh state it is remarkable for its extreme cottony softness and is easily compressed into a wad between the fingers by the slightest pressure. It remains sterile for weeks, as it develops rather slowly, but at length forms a hymenium from the center outward, the surface of which becomes labyrinthiform-wrinkled with shallow, obtuse wrinkles. The margin for some distance remains sterile a long time. On the dryer, the wrinkles disappear and the whole plant takes on a creamy-yellowish color. In the early stages of development, it may be entirely resupinate, either narrowly or broadly, depending on its position with respect to gravity. If attached to a vertical support, it has a conchate shape, often confluent laterally, and is elongated to a narrow base. The context is about 1 mm. thick. The surface of the reflexed portion is at first appressed cottony, then pruinose and subtomentose on margin. The spores measure 4–5 × 1 μ, and are hyaline, allantoid and smooth. There are no cystidia. The basidia are small, 16–18 × 3.5–4 μ, forming a dense hymenium, 4-spored. The size range given by Burt (*l. c.*) is too small for this western form; it varies from 2–4 cm. to 3–6 cm. in its different diameters. Odor and taste none when fresh. One gets the impression that the plants are much softer than those found in the eastern United States, although this may be due entirely to weather conditions.

PHLEBIA ALBIDA Fr. — On oak wood.

PHLEBIA CINNABARINA Schw. — On bark of *Alnus oregona.*

PHLEBIA RADIATA Fr. — On bark of oak.

POLYPOREAE

FOMES IGNIARIUS Fr. — On Alnus. Infrequent.

FOMES PINICOLA Fr. —On Douglas fir, frequent.

LENZITES BETULINA Fr. — On oak stumps.

LENZITES SEPIARIA Fr. — On wood of western yellow pine and Douglas fir.

POLYPORUS BIFORMIS Klotzsch. — On oak log.

POLYPORUS CAESIUS Fr. —On decayed wood of western yellow pine. Infrequent.

POLYPORUS FRAGILIS Fr. — On western yellow pine and Douglas fir.

Polyporus pacificus Kauff., sp. nov. (Plates XXIV–XXVI). — CARPOPHORE with multiplex-cespitose pilei which arise from a common stout stem; the stem in turn arises from a sclerotium or a sclerotoid large base imbedded deep in humus or in dead rotten wood close to roots or trunks of conifers. The entire pileate mass measures 15–25 (40) cm. across the top. It has a height of 20–30 cm. above the ground.

PILEI fleshy, 5–10 cm. in diam., expanded-depressed, central ones orbicular with central secondary pilei, lateral pilei flabelliform to spatulate and loosely imbricate, with confluent secondary stems of flattened shape, all arising from a confluent single stem; surface *whitish,* radially very rugose-fibrous, center villose-fibrose and cristate, glabrous elsewhere; margin at maturity thin, acute and sterile (2 mm.). CONTEXT thick at broad center, thin on margin, *white,* radially very fibrous and easily split, tough across radial, very scissile (horizontally), and *watery-spongy when fresh.* TUBES 3–10 mm. long, short on margin, longer toward stem, rather easily removable from context, *white at first,* slowly "cartridge-buff" (R.), becoming sordid when bruised, decurrent, terminating at beginning of the stem system; pores angular, becoming subsinuate-subdedaloid, *large,* 1–2 per mm., dissepiments thin, entire. STEM simple below, stout, 20–40 mm. in diam., dilated upward and branching above, solid, with an irregularly undulate surface, *dull whitish*, becoming sordid in age, concolorous within, lower portion sometimes deeply imbedded (4–6 cm.). SCLEROTIUM irregularly globose (perhaps variable), about 7–8 cm. in diam., white within, sordid externally, compact. SPORES broadly elliptical, *smooth*, hyaline, 5–6 × 3.5–4 μ. CYSTIDIA *very abundant* in the hymenium, fusiform, acutely pointed, hyaline, thin-walled, nearly twice the length of the basidia. ODOR none or very slightly subacid; taste none.

Type collected by C. H. Kauffman in forests of Douglas fir and western hemlock, Lake Quiniault, Washington, October 20, 1925.

This Polyporus belongs to the section Grifola; if the latter is used as a genus the name is *Grifola pacifica.* It was seen several times at Lake Quiniault and studied at various stages of development and age. It was also collected at Takilma, Oregon, December 10, 1925. It may grow out of the deep humus, apparently from some subterranean root, but reaches its largest size on the ground adjoining large conifer trunks or stumps. It sometimes grows at the base of rotten trees or even through rotten cracks in the trunk above the ground; in the latter place it forms a large fleshy mass in the crack from which the secondary stems arise. The fibers of the pilei lie parallel and in the center of the pileus grow more or less vertically to the surface, forming cristate tufts much as in *P. borealis* Fr. The younger plants have a thick pileus with obtuse margin, which as they mature becomes rapidly thinner toward the margin. From *P. giganteus* Fr., to which it seems most closely allied, our plant differs by its numerous cystidia, its non-globose spores, the white color which does not turn black on the pore-surface, the more numerous pilei as a rule and the nature of the surface and context of the pilei. The other American species of the section Grifola need scarcely be compared; neither they nor *P. giganteus* occur associated with coniferous trees.

POLYPORUS PERENNIS Fr. — On burned soil under conifers.

POLYPORUS SCHWEINITZII Fr. — On Douglas fir.

POLYPORUS VARIUS Fr. — On decorticated fallen branches and sticks of coniferous wood.

POLYPORUS URSINUS Lloyd. — On wood of Douglas fir.

TRAMETES ABIETIS Karst. — On rotten coniferous wood.

TRAMETES CARNEA Nees. — On Douglas fir.

TRAMETES PINI Fr. — On living Douglas fir.

TRAMETES SEPIUM Berk. — On wood of Madroña tree.

TRAMETES SUBSINUOSA Bres. — On bark of *Abies sp.*, western yellow pine and Douglas fir.

BOLETACEAE

BOLETUS GRANULATUS Fr. — Under firs.

BOLETUS LUTEUS Fr. — Under oak leaves in mixed forest.

AGARICACEAE

AMANITA CALYPTRATOIDES Pk. — In mixed forest of oak and conifers. Peck's description omits mention of the thick double volvate cup at base of stem. A single specimen was found.

CANTHERELLUS CIBARIUS Fr. — Seen only once.

CLAUDOPUS

A synopsis and discussion of the known American species, with special reference to Pacific Coast plants, seems desirable.

Only about thirty-five species of Claudopus have been described. Murrill (20) recognizes nine of these for North America. The writer is presenting below four additional species, collected in the northwestern Pacific portion of the United States.

The genus has recently been disrupted by several authors, the segregation being made on the basis of whether the spores are angular or even. Thus, Rea (24), following Ricken (25), has placed the even-spored species in the genus Crepidotus, notwithstanding the fact that the spore color of these plants is pink instead of ochraceous. The angular-spored forms are retained in the emended genus Claudopus. Lange (16), following Quélet (23) and Schroeter (27), treats all the pink-spored group as a single genus "Rhodophyllus," and includes only angular-spored plants. In doing so, he is compelled to split the genus Clitopilus, and to remove the genus Pluteus. The genus Claudopus is not mentioned, but since both kinds of spores occur, it, too, would be split like Clitopilus. As Bresadola and others have remarked, such readjustments of the generic values as established by Fries cause much more difficult questions to arise in connection with the excluded species and can end only in a multiplication of genera whose coherence will be based on slender connections.

We have, apparently, a majority of even-spored species in the genus Claudopus in this country. Five species are reported to be angular-spored. To separate these two groups as subgenera or sections within the genus should serve every purpose.

The known North American species are keyed out below, with comments on those known to the writer. *C. subnidulans* Overholts is without doubt *Crepidotus dorsalis* Pk. and *C. mephiticus* Murr. of which the writer received cotype material from the finder in Minnesota, does not appear to be a good Claudopus.

KEY TO THE AMERICAN SPECIES OF CLAUDOPUS

1. Spores even.. 2
1. Spores angular, ellipsoid in outline; stipitate...................... 7
2. Pileus 3–7 cm. broad, yellow, tinged with orange or salmon, sessile *C. nidulans* Fr.
2. Pileus small, not over 3 cm. broad; not yellow................... 3
3. Spores elongated.. 4
3. Spores globose; pileus white, then alutaceous, 4–6 mm. broad, sessile..............................*C. cortinicinctus*, sp. nov.
4. Pileus persistently white, substipitate.......................... 5
4. Pileus not white, or white at first and becoming tinted, sessile...... 6
5. Spores 7–8 (9) × 4–5 μ.......................*C. variabilis* Fr.–Bres.
5. Spores 6–7 (8) × 2–3 μ..........................*C. commixtus* Bres.
6. Spores elliptic-lanceolate, 7–8 × 3.5–4 μ, pointed at one end; pileus clay color to cinnamon-buff...............*C. subargillaceus*, sp. nov.
6. Spores broadly ellipsoid, 6–7 × 4 μ, obtuse; pileus at first white, changing to pale pinkish-cinnamon................*C. affinis*, sp. nov.
7. Pileus minute, 1–4 mm., white; spores 7–12 × 6–8 μ................. *C. subdepluens* Fitzpatrick
7. Pileus 5–15 (25) mm.. 8

8. Pileus whitish with pinkish or rufescent villosity; gills broad; spores 9–11 × 6–8 μ.............................*C. depluens* Fr.–Rea.

8. Pileus gray, grayish-cinnamon, pale drab or brown.............. 9

9. Pileus pale drab, minutely tomentose; gills broad, distant; stem short, tomentose; spores 8–10 × 5–6 μ (Oregon)..*C. avellaneus* Murr.

9. Pileus grayish or brown.. 10

10. Gills subdecurrent; pileus covered with a fine pruinosity, not hygrophanous; spores 9–11 × 6–7 μ................*C. byssisedus* Fr.

10. Gills free; pileus hygrophanous; spores 8.5–11 × 7.5 μ (New York).................................*C. griegensis* (Pk.) Sacc.

Claudopus affinis Kauff., sp. nov. — Pileus submembranous, semiorbicular, convex-plane, at length ascending, reflexed at maturity, sessile by a narrow base, white, gradually assuming a "pale pinkish cinnamon" (R.) color except the persistently white and thin tomentosity, which is more dense posteriorly; margin even, at first incurved, then spreading. Gills radiating from a point, of medium width (2–2.5 mm.), close, thin, at first white, becoming a clear flesh color at maturity, simple, edge entire. Spores elliptic-lanceolate, pointed at one end, smooth, subhyaline, epispore with a faint tint of clear pink under microscope, 7–8 × 3.5–4 μ. Cystidia none. Sterile cells lacking on edge of gills.

Type collected by C. H. Kauffman, on bark of dead oak trunk, at Takilma, Oregon, December 6, 1925.

The plants have the appearance, in habit and size, of *Pleurotus septicus* Fr., but with smaller, narrower and pointed spores which are tinged pink. The change of the pileus from white to pinkish-cinnamon recalls *Claudopus depluens* (Batsch), but the latter species has large and angular spores. It is entirely possible that I missed the sterile cells on the edge of the gills, but they were carefully looked for.

Claudopus cortinicinctus Kauff., sp. nov. — Pileus 4–6 (10) mm. broad, subfleshy, sessile, at first cupulate-resupinate, remaining resupinate on under side of substratum, becoming conchoid-ascending elsewhere, arising from a cobwebby white subiculum, with zone of radiating white fibrils at point of attachment, the conchate pileus compressed laterally, white at first, becoming alutaceous, surface silky or downy; margin incurved and membranous, even. Gills radiating from a point, very narrow, close to subdistant, pink then sordid, edge entire. SPORES spherical, minutely tubercular under high power of microscope, tinged distinctly buff-pink, 4–5 μ in diam.; cystidia none; no sterile cells observed; gill-trama composed of compact, subgelatinous, subparallel hyphae; trama of pileus subgelatinous, the lower half composed of compact parallel hyphae, the upper half of loose floccose hyphae.

Type collected by C. H. Kauffman, on bark of dead vine maple branches on a brush heap in the forest, at Lake Quiniault, Washington, October 22, 1925.

On drying the pileus curls and folds inward owing doubtless to the subgelatinous context. It is soft when fresh, slightly tough when dry. *Crepidotus applanatus*, of which this might appear to be a small form, differs in its more crowded gills, larger size, hygrophanous pileus, and its smooth, ochraceous-tinted spores.

CLAUDOPUS COMMIXTUS Bres. — The plants placed here have the following characters: PILEUS 4–15 mm. broad, slightly fleshy, at first laterally extended, soon resupinate, white, dull, conchoid, at length flattened, surface innately silky-pubescent, even on margin; flesh thin, white. GILLS radiating from a point, rather broad, ventricose, subdistant to close, at first white, soon incarnate-tinted. SPORES under the microscope hyaline, tinted incarnate in mass, narrowly oblong, slightly curved, i.e., one side subdepressed, 6–7 (8) × 2-2.5 μ; cystidia none; no sterile cells seen; basidia 20 × 5 μ, 4-spored.

On bark, petioles, fallen leaves and twigs of maple and conifers. Collected by C. H. Kauffman at Lake Quiniault, Washington, October 17, 1925.

Our collection departs from the description of Bresadola (see Saccardo, *Syll.*, 21:149) only in the fact that the young pilei, at least on twigs, extend horizontally; the older pilei become resupinate, as on the broad surfaces of maple leaves.

CLAUDOPUS NIDULANS Fr. (Plate XXVII). — On dead trunk and stumps of yellow pine. Several collections were studied with a view to determine the answer to the question why there have been reports that this species has no odor. On November 18, during collecting near Corvallis, Oregon, fine fresh material in all the different stages of development and maturity was brought in, carefully tested for odor, then allowed to lie exposed on the table overnight and tested again. None of this lot during this time had any traces of the usual characteristic odor which one associates with this plant. In this collection the spores measured 5–7 × 3–3.5 μ. On December 8, at Takilma, a large collection, growing on a 12-foot pine stub, was brought in and also was found to be without odor in the fresh condition. But after these were placed over the heater to dry, the characteristic evil odor began to be strongly manifest. In the Adirondack Mountains in 1921, during the drying of a cluster over the heater in the closed workroom of a building, the odor became almost unbearable until the doors were opened. On the other hand, Murrill (*Mycologia*, 7: 300. 1915) reports that a collection made from conifer wood at Lake Placid in the Adirondack Mountains and tested by a number of people besides himself, "had no mephitic odor," and he states he had never found it with an odor. It seems clear that we have here a plant in which certain changes occur when the fungus dries either *in situ* or over artificial heat, and that the disagreeable and strong odor sometimes noted by me in the field, but more evident in the drying oven, is the result of chemical changes, more or less rapid, which correspond to the more or less greater intensity of the odors evolved. In the *Agaricaceae of Michigan*, I have stated that the odor is very disagreeable when the plants are fresh. This statement was based on several experiences in the field. It would appear, however, that weather or growth conditions surrounding a cluster of these plants bring this odor about in some plants and not in others, even when otherwise they appear to be in fresh condition. It is desirable to make extracts of this fungus and study the chemical nature of the substances concerned and their evil-smelling product.

The spores and other microscopic characters, carefully examined, in three of the Oregon collections, are all alike.

There are no cystidia, and no sterile cells on the edge of the gills. The gill-trama is composed of very slender and very compact hyphae.

The basidia also are slender, measure about 35 × 3.5–4 μ and at least some are 4-spored. With the instrument available, although bispored basidia seemed present, this could not be established with certainty. Spore sizes obtained from eastern plants seem to average slightly larger, and we may have two somewhat different forms of this cosmopolitan species. It seems clear, however, that the presence or absence of odor does not figure in this connection. The spore measurements given by Murrill (20) are untenable. His bacillus-like "spores" may well be related to a fermentation process, which in turn may break down substances which are responsible for the odor.

The spore color in mass has led a number of mycologists to place this species in Crepidotus. Fries had it in Pleurotus. Under the higher powers of the microscope, the spore wall of fresh spores is pinkish, not as clear and delicate as in many of the pink-spored species. Rea (24) places it in Crepidotus, with which it doubtless has affinities. In our western plants the gills are thickish, occasionally forked, more or less discrete and, at least toward the margin, easily separable from the trama of pileus. These characters indicate Paxillus relationships. Not all collections show these points, however, and manuals omit mention of them.

A paper, by R. Singer (29), has just come to hand, in which this species is discussed in its European aspects; it is called *Pleurotus nidulans* (Pers.) Fr. The discussion concerns itself mostly with the spore color. Quélet (23), under the name *Crepidotus Jonquillea*, seems to have been the first to note that the spores have a mixture of rosy and ochraceous color. Singer (*l. c.*) refers *Claudopus odorativus* Britz. to the species in question. Britzelmayr says "sporen rosenrot." Singer gives the color of the spore-mass on white paper as "fleischrosa," and the size 5.5–7.2 × 3.5 μ. Its distribution, according to this same author, is Sweden, France, Austria and

Germany; to these we may add the northern United States and Canada.

Singer considers it a Pleurotus with rosy spores because the spores are not angular, i.e., only angular-spored species are for him — and for some others — species of Claudopus. He shies, however, at setting up a new genus. The odor is said to be melon-like, somewhat of "sauerkraut." It is clear to me that he is dealing with the same species we have, which has been well enough known but not very thoroughly described (but see Kauffman, 8).

CLAUDOPUS SUBARGILLACEUS Kauff., sp. nov. — PILEUS subfleshy, slightly toughish, 2–2.5 cm. broad, sessile, subreniform to suborbicular, subconchate, attached at the slight umbo, ascending, "clay color" (R.), cinnamon-buff toward margin, moist, with a subgelatinous pellicle, even or substriatulate on the membranous margin, very glabrous; flesh thin, concolorous. GILLS radiating from a central point, rather broad, terminating abruptly at the posterior end, close, pallid, then flesh color, edge suberose. SPORES broadly elliptical, smooth, with pink epispore, 6–7 × 4 μ; cystidia none; sterile cells apparently lacking; basidia about 26 × 4 μ, 4-spored.

Type collected by C. H. Kauffman on oak log, Takilma, Oregon, December 5, 1925.

Differs from most species in the non-angular small spores and sessile pileus. The spore characters given by some authors (e.g. Ricken, Rea, Murrill) for *C. variabilis* are similar to those of this species, but our plant was not stipitate, nor do the colors agree. When dried the specimens are brown.

CLAUDOPUS VARIABILIS Fr.–Bres. — This collection is evidently only a *minor form* of this species. PILEUS sessile or with a very short, slender stipe, resupinate, subcircular to slightly reniform, white, surface pruinose, unpolished, even on margin, 3–10 mm. in diam., remaining white when dried. GILLS adnate, of medium width, close, white at first, flesh color at maturity. SPORES broadly elliptical, smooth, with pink epispore, 7–8 × 4–5 μ. Cystidia none. Sterile cells present on edge of gills, about 40 μ long, slender, subfilamentous above, slightly ventricose toward base. Basidia 27–30 × 7–8 μ, 4-spored.

Maire (in Rea) says the spores are warted. According to Bresadola (quoted by Saccardo, *Syll.*, 21 : 149), the spores of *C. variabilis* are even and measure 7–9 × 4–5 μ, and a segregate which he calls *C. commixtus* Bres. (*l. c.*) is described with spores measuring 6–8 × 2–3 μ. The spore size given by Ricken (25) is too small, and shows that the identity of several of the supposedly well-known European species is far from clear.

CLITOCYBE[1]

Clitocybe amara Fr.
Clitocybe (Laccaria) amethystina Bolt.
Clitocybe concava Fr.
Clitocybe conglobatum Vitt.–Bres.
Clitocybe diatreta Fr.–Kauff.
Clitocybe fragrans Fr.–Ricken
Clitocybe (Laccaria) laccata Fr.
Clitocybe odora Fr. var. pacifica Kauff.
Clitocybe phyllophiloides Pk.
Clitocybe piceina Pk.
Clitocybe rivulosa Fr. var. angustifolia Kauff.
Clitocybe Robinsoniae Murr.
Clitocybe suaveolens Fr.–Ricken
Clitocybe subconcava Pk.

COLLYBIA

The Pacific Coast species of Collybia named by Peck and Murrill are not very completely described. Such as have been found and studied by the writer are described in more detail below.

Collybia acervata Fr.
Collybia butyracea Fr.
Collybia cirrhata Fr.
Collybia conigena Fr. (*non* Authors)
Collybia semitalis Fr.

Collybia albogrisea Pk. (*Bull. Torr. Bot. Club*, 22:199. 1895). — Pileus 1.5–2.5 cm. broad, fleshy, thin, convex to subhemispherical, subexpanded, obtuse, brownish-gray when young, "drab-gray" (R.) at maturity, glabrous, almost lubricous, fading to whitish-gray, hygrophanous, striatulate when moist; flesh scissile, concolorous. GILLS broadly adnate, becoming slightly arcuate-subdecurrent, white, broad, subdistant, somewhat intervenose, gradually narrowed to a point anteriorly. STEM 2–5 cm. long, 1.5–3 mm. thick, equal or tapering slightly downward, straight or curved, pale grayish-white, hollow, glabrous above, often confluent and joined below by white or yellowish-gray villose tomentum or merely by hairs. SPORES oblong, hyaline, smooth, 5–6 × 3–3.5 μ; cystidia none; sterile cells on edge of gills abundant, nine-pin-shaped, hyaline, 30–32 × 8–10 μ. ODOR none; taste slight, bitterish.

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[1] For further information on these species of Clitocybe, see Kauffman (11).

Cespitose, among fallen leaves. The Takilma specimens grew out of cracks in the bark of a Douglas fir log. It has somewhat the appearance of *Collybia familia* Pk., but the spores are not globose, and the gills are broad and subdistant. The type was sent to Peck by McClatchie, from Pasadena, California. Our collection establishes its range north into Oregon. In the specimens growing from logs, the tomentum at the base of the stems was much reduced, consisting of a white hairiness around the confluent portions.

COLLYBIA AVELLANEIGRISEA Murr. (*N. A. Flora*, 9 : 369. 1916). — PILEUS 1–2.5 (3) cm. broad, at first campanulate, then subexpanded and obtusely umbonate, with a thin, subseparable gelatinous pellicle, hygrophanous, shining and subviscid when moist, "Saccardo umber" (R.), fading to "avellaneous" or "clay color" on losing moisture, glabrous, margin substriate or even, at first incurved; flesh scissile, concolorous, thin. GILLS adnexed, broad (5–6 mm.), close, grayish-drab, edge concolorous, entire. STEM 3–5 cm. long, 2–4 mm. thick, terete or subcompressed, glabrous, hollow, even, "wood-brown" or avellaneous when moist, white-pubescent at apex, concolorous within, then whitish, tough, cartilaginous, attached to decaying fir needles and humus by white, strigose hairs. SPORES ellipsoid, hyaline, smooth, 7–8 (9) × 3.5–4 μ, subacute at one end; cystidia none; sterile cells not differentiated; basidia 32 × 5 μ. ODOR none or sometimes a faint whiff of meal; taste slight.

Gregarious. The type was collected by Murrill near Seattle, Washington. The Takilma collection is doubtless the same, although, as noted, the pileus has a gelatinous pellicle which accounts for the shining surface in the moist condition, and the plants are hygrophanous, shown not only by the change on fading but by the scissile flesh of the pileus. It differs from *C. ozes* Fr.–Ricken only in its longer spores and glabrous stem.

Collybia solidipes Kauff., sp. nov. — PILEUS 4–8 cm. broad, fleshy, convex-expanded, obtuse or broadly subumbonate, glabrous, even, at first "mouse gray" (R.), paler when mature, "pallid mouse gray," except disk; flesh fragile, whitish or tinted gray. GILLS at first adnate with decurrent tooth, or some subdecurrent, at length sinuate-subdecurrent, broad (7–9 mm.), close, whitish or grayish-tinted, subarid and breaking transversely when old, edge concolorous and entire. STEM 7–10 cm. long, 10–15 mm. thick at apex, tapering downward and elongated-subradicate, *solid*, whitish with gray tinge, glabrous, even or faintly fibrillose-striatulate, cartilaginous, rigid-brittle. SPORES minute, subglobose, 4 × 3 μ in diam., hyaline, smooth; cystidia none; sterile cells not differentiated; basidia 38 × 5 μ, 4-spored. ODOR and taste mild or subfarinaceous. Gregarious.

Type collected by C. H. Kauffman, in mixed forest of oak and sugar pine, Takilma, Oregon, December 10, 1925.

The pileus and stem are neither scaly nor tomentose in any sense, and in this respect, as well as by its colors, the plant differs from *Tricholoma subluridum* Murr. *Tricholoma collybiiforme* Murr. differs by its fulvous pileus and hollow, eccentric stem. *Collybia denticulata* Murr. has a cespitose habit, a hollow and non-rooting stem and umbilicate pileus. All these are said to have the same minute, subglobose spores.

COLLYBIA UMBONATA Pk. (*Bull. Torr. Bot. Club*, 31: 178. 1904). —

PILEUS 4–10 cm. broad, fleshy, conic-campanulate at first, then expanded-plane and umbonate or merely obtuse, "testaceous" or "cacao-brown" (R.), the umbo or disk "bone brown" or blotched with darker shades, with a very thin, gelatinous, separable pellicle, subviscid when wet, glabrous, even on the thin, deflexed margin; flesh in upper portion concolorous, whitish toward gills, moist, 3–5 mm. thick. GILLS narrowly adnexed, abruptly broad behind, gradually narrowed to the front, close (not crowded), white or pallid, edge concolorous and more or less eroded. STEM long-rooting, 10–20 (30) cm. long, 5–15 (20) mm. thick at upper thickest part, tapering more or less regularly down to a point, i.e., the root prolongation becoming very slender, sometimes thickest above the abrupt root, stuffed then hollow, cartilaginous, glabrous, even or rarely subsulcate, whitish but shaded by color of pileus. SPORES elliptical, hyaline, smooth, 6–8 × 3.5–4.5 μ; cystidia none; sterile cells indistinct; basidia 40–42 × 7–8 μ, 4-spored. ODOR of benzaldehyde; taste slowly disagreeable-bitterish.

Growing subcespitosely or scattered on stumps or partially buried wood of conifers. The Takilma plants grew out of cracks of a rotten Douglas fir log. *C. fusipes* Fr. is similar, but its gills are markedly distant and it has different spores. The subviscid character of the pileus is not mentioned by Peck, and inasmuch as the plants were sent to him from California, this is not surprising. Murrill (19) also does not mention this character.

CORTINARIUS ANFRACTUS Fr.
CORTINARIUS ANOMALUS Fr.
CORTINARIUS ISABELLINUS Fr.
CORTINARIUS SEMISANGUINEUS Fr.

FLAMMULA DECORATA Murr. — This species is rather frequent in Oregon and Washington, especially in the mixed conifer and hardwood forests. The smaller specimens of *F. lenta* Fr., a species also frequent, are easily confused with it. In *F. lenta*, however, the stem regularly has a yellowish tint in mature plants and the surface lacks the small persistent fibrillose scales characteristic of the pileus of *F. decorata.* The microscopic characters are very similar in the two species. The range in size of pileus is 3–7 (8) cm. for *F. lenta;* 2–4 (5) cm. for *F. decorata.* The latter more often grows solitary on dead branches and sticks of conifers. Both have a glutinous pileus. In habit and other characters except the colors of the plant and of the spores, *F. lenta* reminds one not a little of *F. polychroa* Berk. of the eastern United States.

FLAMMULA LENTA Fr. — Gregarious, among débris of Douglas fir, attached to needle masses, sticks, old cones and humus. *Hebeloma glutinosa* Fr., with which it is easily confused, is a stouter plant.

FLAMMULA LIQUIRITIAE Fr. — On pieces of rotten conifer wood.

FLAMMULA PENETRANS Fr. — On pine log.

FLAMMULA SUBFULVA Pk. — This is probably best considered a variety of *F. lubrica* Fr. Its pileus is characterized by a "tawny" to "mars brown" (R.) disk, elsewhere "clay color," dotted with "clay color," appressed, fibrillose scales on the glutinous surface. The cystidia have an undulate outline like those of the genuine *F. lubrica.* In the latter the color of the pileus is "zinc orange" instead of "clay color." See Synopsis of this genus *Am. Journ. Bot.*, 13 : 16, 26. 1926.

GALERA HYPNORUM Fr.–Ricken. — Common on mosses in fields and woods, also on mosses growing on tree trunks.

GALERA PYGMAEA-AFFINIS Fr.–Ricken. — On cow dung.

GALERA SPICULA (Lasch.) Ricken. — Among grass and moss in pasture.

GOMPHIDIUS OREGONENSIS Pk. — As pointed out in a previous paper (9), this species was known to the writer only by a few collections from the mountain districts of Idaho, Washington and Oregon, and the suggestion was offered that it was much less abundant in Oregon than had been reported. On the present occasion, however, it was seen in fair abundance, both about Corvallis, Oregon, and at Takilma. Its distribution evidently is greater in frondose woods or mixed woods out in the great valleys, and along the lower elevations of the Siskiyou country. I have found it but rarely in the deep coniferous mountain forests. In small plants the stem above the annulus is frequently white.

GOMPHIDIUS SUBROSEUS Kauff. (9). — Under Douglas fir.

HEBELOMA SERICIPES Earle (*Bull. N. Y. Bot. Gard.*, 2 : 342. 1902). — This collection appears to belong to the same species which Earle described from a collection made at Stanford University, California. A more complete description follows: PILEUS 4–7 cm. broad, fleshy, but toughish and pliant, convex-plane or subdepressed, obtuse, viscid when wet and fresh, deep "honey yellow" (R.), glabrous, margin silky-fibrillose; flesh concolorous (moist), whitish (dry). GILLS adnate then sinuate, crowded, narrow, whitish at first then "avellaneous" (R.), edge white-flocculose from the prominent sterile cells. STEM 4–8 cm. long, 6–9 mm. thick, equal or tapering slightly upward, coated by a conspicuous white silky-fibrillose sheath, apex floccose, subglabrescent in age and becoming fuscescent downward, at first subrigid-subelastic. SPORES ellipsoid-ovoid, 8–10 × 5–6 (7) μ, inequilateral, smooth; cystidia none; sterile cells broadly filamentous, 50–70 × 5–7 μ, hyaline. ODOR "like chestnut flowers" or none; taste none.

The type grew among oak leaves. The Takilma plants grew under oak and fir, collected December 12, 1925.

Earle described the stem as solid. It is likely that this discrepancy is due to error. The Takilma plants grew in places where *Flammula lenta* and *Stropharia Sienna* Pk. were abundant, and the colors of these three are quite similar in young plants; however, the pilei of the latter two species are covered by superficial scales, and the spores differ distinctly.

HEBELOMA TESTACEUM Fr.–Ricken. — PILEUS dull red brown, almost "hazel" (R.). SPORES broadly elliptical, pale, smooth, 10–13 × 5.5–7 μ; cystidia none; sterile cells slender flask-shaped, neck cylindrical, apex rounded, hyaline, 50–60 × 7–14 μ; basidia 40 × 9–10 μ, 4-spored. Under yellow pine and cedar, on the ground. There is some doubt whether this is the Friesian species.

HYGROPHORUS CHRYSODON Fr.
HYGROPHORUS CONICUS Fr.
HYGROPHORUS EBERNEUS Fr.
HYPHOLOMA FASCICULARE Fr.
HYGROPHORUS FUSCOALBUS var. OCCIDENTALIS Kauff.
HYGROPHORUS HYPOTHEJUS Fr.

Hypholoma inocybeforme Kauff., sp. nov. — PILEUS 2.5–4 (5) cm. broad, fleshy, brittle, campanulate, subexpanded or repand, broadly umbonate, *hygrophanous*, "cream-buff" (R.) when young, "chamois" when older but still moist, paler when dry, even, entirely glabrous, only the extreme margin provided with small, appendiculate, white and evanescent veil-remnants; flesh thin except on disk, concolorous, scissile. GILLS narrowly adnate, crowded, narrow (2.5–3.5 mm.), white at first, slowly pale avellaneous to grayish, edge minutely flocculose. STEM 4–6 (7) cm. long, 5–6 mm. thick, equal, white or hyaline-white, apex lacerate-scurfy, minutely silky-floccose to glabrescent downward, hollow, even or rarely striatulate at apex, concolorous within. SPORES oblong, rounded-obtuse at ends, smooth, 7–8 × 4–4.5 μ, bright brownish-purple under microscope; cystidia none; sterile cells on edge of gills saccate-clavate, tapering to slender pedicel, rounded at apex, hyaline, thin-walled, 42–46 μ long, 10–14 μ thick above. ODOR none or slightly aromatic; taste slight.

Type collected by C. H. Kauffman, along roadside banks in clay soil, conifer and oak forest, Takilma, Oregon, December 12, 1925.

This is distinct by its lack of cystidia, the clavate sterile cells, pale colors and broad umbo. The delicate snow-white appendiculate veil-remnants are seen only in young partly expanded plants. The wet pileus sometimes becomes radiately rugose on drying out. The shape, colors (especially of gills) and habit suggest an Inocybe; the spore color and appendiculate pileus show it to be a Hypholoma.

INOCYBE ALBODISCA Pk.
INOCYBE GEOPHYLLA Fr.
INOCYBE LILACINA (Boud.) Kauff.
INOCYBE RETIPES Atk.
INOCYBE SORORIA Kauff.

Inocybe siskiyouensis Kauff., sp. nov. — PILEUS subfleshy, 2–4 cm. broad, campanulate, expanded-umbonate, pale tawny-ochraceous, umbo yellowish, innately silky, at length rimulose on margin; flesh concolorous. GILLS adnate, seceding, rather narrow, subventricose, close, at first whitish, then "clay color" (R.), edge white-fimbriate. STEM 3–4 (5) cm. long, 5–7 mm. thick, curved or straight, with a rounded subemarginate bulb at base, equal above bulb, terete or subcompressed, pallid or whitish, solid. SPORES subellipsoid, smooth, inequilateral, 7–8 (9) $\times$ 4–5 μ, ochraceous under microscope; cystidia obese, 50 $\times$ 10–13 μ, subventricose below, with stout neck, thick-walled and thin-walled, scattered on sides and edge of gills, not abundant. ODOR slight, specific. Gregarious.

Type collected by C. H. Kauffman, under fir and oak, Takilma, Oregon, in the Siskiyou Mountains, December 7, 1925.

This species has many of the characters of *I. Cookei* Berk., but possesses cystidia on the gills.

LACTARIUS DELICIOSUS Fr. — Good examples were found at Takilma. After extensive observations of this species in the mountain regions of the West, including Colorado, Wyoming, Montana, Idaho, Washington and Oregon, it is clear to me that in this wide region the plants have some aberrant appearances. Ever since this was noticed, studies have been made of fresh collections to determine whether any morphological characters could be the basis for such impressions. In the frondose woods of southern Michigan, and generally in the eastern United States, during rainy weather, the plants average large, with a pileus 5–10 (12) cm. broad. This size is unusual in the drier conifer forests of the West, as in Wyoming and Colorado, where the average size of the pileus is 5–6 cm. Along the moist Pacific slopes, however, the larger plants are more common. The development in conifer forests, where the ground is often hard and covered by a layer of needles, is slow either because of the nature of the soil or the closely packed cover, and one seldom finds plants which when broken yield copious orange milk. Usually the milk is scanty or cannot be seen. Furthermore, the zones on the surface of the pileus in many regions are only faintly marked or else non-existent. But, even though the milk is not manifest, the plants, when otherwise fresh, turn to "jade-green" or "hellebore green" (R.) at broken or bruised places, or, as in most of them, the development has apparently been slow and the surface of the plants, as well as the flesh, has already taken on these greenish-olivaceous tints and is much variegated. The characteristics mentioned above give the collector a feeling that the plants are not *L. deliciosus*.

The colors, in general, are different from those of the same species in Europe. Invariably the European plants are described as reddish-orange, and, in those Icones in which the color of the figures is well reproduced, show a more reddish or salmon color than occurs in American plants. A glance at Bresadola's (3) recently published plate (Pl. 373) shows the difference at once. Like Fries, in *Hymenomycetes Europaei*, Bresadola says the pileus and stem are "testaceous-aurantiaceous." The colors shown in Bresadola's plate are mainly "rufous" when compared with Ridgway.

The pileus, gills and stem of our western plants, in a perfectly fresh condition (and largely the same in the East), are "orange buff" (R.) to "ochraceous orange" and lack the "testaceous" and "rufous" color; the gills and stem are often "xanthine orange" or become so. Very soon, however, the greenish-olivaceous stains or tints come to the foreground.

Peck (21) separated his species, *L. chelidonium* Pk., from *L. deliciosus* by its paler milk, "saffron yellow," the dull color of the pileus, the narrow gills, short stem and its fondness for dry situations; bluish stains are said to precede the greenish. The gills of *L. deliciosus* are practically always narrow, the stems in the drier mountain·forests are generally short or very short, and bluish tints are frequently mixed with the green. I have seen the most striking mixture of colors in plants I collected at Ithaca, New York. These characters, as well as the differences in the shade of yellow which the milk possesses, lead me to consider *L. chelidonium* as an untenable species, to which one can, from its description, occasionally refer a collection, but which has no sound specific characters. Peck himself (*l. c.*) was not very confident of its validity. *L. deliciosus*, barring genetic variations nonspecific in a taxonomic sense, is thus seen to be a highly variable species, influenced to large degrees by conditions of moisture, soil and temperature.

LACTARIUS NITIDUS Burl. — These western specimens differ slightly in the paler colors of pileus and stem and the rather narrow gills.

LACTARIUS THEIOGALUS Fr.
LACTARIUS UVIDUS Fr.
LEPIOTA ACERINA Pk.
LEPIOTA CRISTATA Fr.
LEPIOTA GLATFELTERI Pk.
LEPIOTA RUGOSO-RETICULATA Lorin

LEPIOTA ROSEIFOLIA Murr. (*Mycologia*, 4:235. 1912). — This species, described from La Honda, California, by Murrill, should be more fully described. PILEUS 4–6 cm. broad, fleshy, fragile, campanulate, then expanded-umbonate, umbo broad and obtuse, cuticle umber to chestnut-colored, becoming innately appressed-scaly and radially rimose except on umbo, changing to orange-reddish where bruised, disk sometimes almost blackish, margin even; flesh white, rather thin, changing to pinkish where cut. GILLS free, remote when pileus is expanded, crowded, rather narrow (4–6 mm.), changing to pinkish where touched, edge concolorous, minutely fimbriate. STEM 8–12 (17) cm. long, 5–7 mm. thick, equal or slightly incrassate downward, stuffed with a loose white pith, surface dingy avellaneous, rufescent, concolorous within, naked at apex, minutely fibrillose-reticulate then glabrous up to the ring. ANNULUS membranous, rather distant, white, at first ascending-flaring, then decurved, whitish, with a distinct blackish edge, entirely blackening on drying. SPORES ellipsoid-subventricose, hyaline, smooth, 6–7 (8) × 3.5–4 μ; cystidia none; sterile cells broadly clavate, rounded at apex, hyaline, tapering to base, 35–40 μ long, 11–13 μ thick at apex; gill-trama interwoven. ODOR none; taste mild.

Reported by Murrill as growing in a redwood forest; collected by the writer also near Corvallis, Oregon, November 19, 1925.

LEPTONIA ASPRELLA Fr.

LEPTONIA PLACIDA Fr.

Leptonia fusciceps Kauff., sp. nov. — PILEUS 2–6 cm. broad, fragile, somewhat fleshy, at first campanulate, then expanded umbonate, the umbo disappearing, often plane or depressed, "fuscous black" (R.) or "fuscous" and even when moist, hygrophanous, "vinaceous-buff" after losing moisture, glabrous, silky-shining (moist), margin at first incurved; flesh thin (1 mm.), concolorous. GILLS very deeply emarginate, narrowly adnexed, broad (5–8 mm.), close, thin, at first gray-tinged, then "drab-gray" or "cinnamon-drab" (R.). STEM 4–7 (8) cm. long, 4–8 mm. thick, cartilaginous, equal or slightly incrassate downward when young, hollow, often twisted and compressed, glabrous, fuscous or paler, innately white-streaked when dry, apex naked. SPORES subglobose, angular, angles not prominent, 8–9 (10) μ with apiculus, pale pinkish with a gray tint under microscope; cystidia none; sterile cells on edge of gills not differentiated. ODOR and taste distinctly farinaceous.

Type collected by C. H. Kauffman, among grass in open places, Lake Quiniault, Washington, October 30, 1925. Found also at Takilma, Oregon, November 29, 1925, in grassy meadows.

This species has a superficial similarity to several described Pacific Coast species. It differs from *L. nigra* Murr. by its subglobose spores and hygrophanous flesh; from *L. fuliginosa* Murr. by its hollow stem, much larger size, the even margin of the pileus, and deeply emarginate gills. Both of Murrill's species were collected at Palo Alto, California. It also departs widely from the better known species of eastern North America and of Europe. The margin of the pileus in our plant becomes undulate-lobed and easily splits on drying or in age. The farinaceous odor and taste are distinctive.

MARASMIUS ANDROSACEUS Fr.

MARASMIUS COHAERENS Fr.

MARASMIUS TOMENTOSIPES Pk.

MYCENA

The genus Mycena is abundantly represented in this region, and, in spite of the lateness of the season, kept appearing in quantity during the mild days that followed the intermittent frosts. Several revised descriptions, bringing the microscopic data into evidence, are presented below. Some species, such as *M. alkalina* Fr. and *M. ammoniaca* Fr., *M. vulgaris* Fr. and *M. plicata* (Schaeff.) (*M. epipterygia*), were very abundant.

MYCENA ALKALINA Fr.

MYCENA AMMONIACA Fr.

MYCENA AURANTIIDISCA Murr. — PILEUS 3–7 mm. broad, membranous, conic-campanulate, subumbonate, moist, "orange" (R.) or reddish-orange when young, then "cadmium yellow," fading to citrine-yellow or whitish, striatulate to umbo, covered with microscopic, short glandular hairs; flesh concolorous. GILLS adnate, narrow, subdistant, white or whitish, edge concolorous. STEM filiform, 1.5–3 cm. long, less than 0.5 mm. thick, golden yellow or orange, fading like pileus, covered by minute glandular hairs. SPORES lanceolate, rounded at one end, pointed at other end, hyaline, smooth, 6–8 × 2.5–3 μ; cystidia none; sterile cells on edge of gills small, a little longer than hymenial cells, 32–35 × 7–9 μ, ventricose, apex rounded, with pale yellow content. Attached to needles of fir, of pine, or on decayed oak leaves and débris.

This was collected and named by Murrill from Mill City, Oregon. Its glandular, although very minute, hairs tend to give the pileus and stem a slightly viscid feel. It grows densely gregarious. In its marked change in color as it develops and afterward as it loses moisture, it differs from *M. aurantiacus* Murr. By its microscopic characters it departs from species of similar appearance. It belongs to the section Filipedes. Perhaps the edges of the gills are sometimes yellow-tinted.

MYCENA "EPIPTERYGIA Fr." *et al.* — A plant, very common all over the needle beds of western yellow pine, is here placed under the group name to which it undoubtedly belongs. Briefly, the pileus is 1.5–2 (3) cm. broad, with a glutinous, separable, olive-buff to umber pellicle. The gills are adnate with a distinct decurrent tooth, narrow and pallid or slightly incarnate-tinted. The stem is 4–8 cm. long × 1–2 mm. thick, equal, pale citrine-yellow, fading to whitish, very glutinous from the separable pellicle, attached at base to the needles. The odor is distinct, somewhat of rancid tallow, occasionally rancid-farinaceous. The spores measure 8–10 (11–12) × 4–5 μ, and are ellipsoid, smooth and hyaline. Basidia are 4-spored. No specialized sterile cells were seen, as the edge of the gills is covered by a slimy filament.

This agrees with *Mycena plicata* (Schaeff.) Bres. (*Iconographia*, Pl. 253). It cannot be placed safely under *M. viscosa* Maire. Maire segregated his species from *M. epipterygia* Authors. He considered the genuine *M. epipterygia* Fr. to be limited to frondose woods. *M. viscosa* has, then, its habitat in conifer forests. The spores of our plant, however, have the size of his typical *M. epipterygia* of frondose woods, only very occasionally reaching 11 or 12 μ long. These larger spores, also, may be in the first stage of germination. Lange (15) gives the spore size 8–9 × 4–4.5 μ, and so does von Höhnel. The true *M. epipterygia*, according to Bresadola, has much broader spores.

MYCENA FLAVO-ALBA Fr.–Ricken. — This is another common species in the conifer forests of Washington and Oregon, appearing apparently late in October and continuing through November and December.

MYCENA GALERICULATA Fr. — On oak logs.

Mycena griseiconica Kauff., sp. nov. — PILEUS fleshy, thin, 1–2.5 cm. high and wide, at first narrowly elliptic-conical, then broadly conical to campanulate, terminating in an obtuse conical umbo, bluish-gray and striatulate to umbo when young or moist, silvery grayish and slightly rugose-wrinkled when dry, scarcely hygrophanous, glabrous. GILLS ascending-arcuate, narrow (2–2.5 mm.), adnate, subdistant, scarcely intervenose. STEM 5–10 cm. long, 1–2 mm. thick, equal, glabrous, naked at apex, *even*, cartilaginous, hollow, colors as in pileus. SPORES elliptical, hyaline, smooth, obtuse, 10–12 (13–14) × 4.5–5.5 (6) μ; cystidia none; sterile cells hyaline, prominent on edge of gills, 40–50 × 9–14 μ, oblanceolate or oboval above and tapering to pedicel, the rounded apex provided with an abrupt slender, cylindrical prolongation (sometimes two) which is 8–12 μ long, 1.5–2 thick. Subcespitose.

Type collected by C. H. Kauffman, on débris in forest of Douglas fir, in the Siskiyou National Forest, Takilma, Oregon, November 27, 1925.

A record of the odor and taste was unfortunately not obtained, but apparently the odor was not noticeable. It is related to such species as *M. polygramma* Fr., *M. vitilis* Fr. and Kauffman's *M. polygramma* var. *albida* (8). From *M. polygramma* Fr.–Rea it differs only by its much narrower spores, the even, non-sulcate stem and the colors of the pileus. Ricken's *M. polygramma* has much smaller spores, although the stem of his plant is also "sulcate-striate." The sterile cells on the edge of the gills, as described by both these authors, are like those of our plant. Several varieties or forms of *M. polygramma* have already been described. Thus, Lange (15) has named two forms: f. *candida* and f. *pumila*. His description of the sterile cells, apparently small in size, is not convincing. It would seem best to segregate our Pacific Coast plant, as I have done. Beardslee (1) gives a description of a plant from Ontario whose spores bar it from *M. polygramma*. No *bona fide* collection of the Friesian species seems to have been made in North America and clearly described as such, and Murrill (19) has properly excluded it from our flora. It must be remembered, however, that even prominent European mycologists do not agree in important details in their studies of *M. polygramma*. Our plant belongs to the Rigidipedes.

MYCENA HAEMATOPODA Fr.
MYCENA LUDEA Fr.–Ricken
MYCENA PLICOSA (Schaeff.) Bres.
MYCENA PURA Fr.
MYCENA PURPUREOFUSCA Pk.
MYCENA ROSELLA Fr.
MYCENA SANGUINOLENTA Fr.
MYCENA VULGARIS Fr.
NAUCORIA CALIFORNICA Murr.
NAUCORIA CENTUNCULA Fr.
NAUCORIA CIDARIS Ricken (*non* Fr.)
NAUCORIA PUBESCENS Murr.
NAUCORIA SIDEROIDES Fr.–Ricken

Omphalia apiculata Kauff., sp. nov. — PILEUS 4–8 mm. broad, submembranous, fragile, subhemispherical, usually with a minute papilla at apex, slightly striatulate when fresh, soon even, subglabrous, white at first, soon changing to creamy-buff; flesh concolorous. GILLS adnate to short decurrent, subarcuate, *narrow*, subdistant to distant, white to pallid. STEM 2.5–3 cm. long, filiform, equal, straight, hyaline-white (becoming yellowish after plants are dried), minutely pubescent its entire length by microscopic short hairs, even. SPORES oval but pointed at one end, smooth, hyaline, minute, 4–5 × 3–3.5 μ; cystidia none; sterile cells not differentiated. ODOR none. Gregarious.

Type collected in fir forest by C. H. Kauffman, Takilma, Oregon, December 2, 1925.

The stems are attached to fir needles from which they are easily detached, and are almost insititious. The margin of the young pileus is straight and appressed on the stem and hence it belongs to the section Mycenarii of Fries. It is related to *O. integrella* Fr., but the pileus is not umbilicate and the gills not narrowly fold-like; in its color changes and spores it differs also. *O. cuspidata* Quél. is a smaller and different plant also.

OMPHALIA BAKERI Murr. — Described from California, but no spore characters are given. It appears to me, however, that the following description of a Takilma species applies to it.

PILEUS 3–10 mm. broad, submembranous, dry, hemispherical to broadly campanulate, unexpanded, obtuse, grayish-avellaneous, fuscous at center, with paler striae, at length subumbilicate and striate-sulcate; flesh whitish and very thin. GILLS adnate-subdecurrent, *broad*, subdistant, white. STEM 2–3 cm. × 1 mm., filiform, equal, glabrous, even, pallid or tinted avellaneous, hollow, cartilaginous. SPORES elliptical, smooth, hyaline, 6–7 × 4 μ; cystidia none. ODOR none. Gregarious and attached to fir needles in a grove of fir trees.

Although *O. Bakeri* is said to occur attached to pine needles, our plant is very possibly the same species.

OMPHALIA HEPATICA (Batsch) Fr. — This species occurred quite extensively in the open grassy valley at Takilma after warm rains. When first studied it was referred to *O. pyxidata* Fr. European mycologists do not agree on the spore characters of the latter species, e.g., Ricken and de Seynes assign echinulate globose spores to it; Rea gives elliptical spores, measuring 6–7 × 4–5 μ; Bresadola, in his latest work (3), assigns broadly elliptical spores to it, said to measure 8–10 × 5–6 μ; while in this country Murrill uses the name *O. subhepatica* (Batsch) and gives the spore size as 6–7.5 × 4–5 μ. On the other hand, both Ricken and Bresadola give the spore size for *O. hepatica* (Batsch) as 6–7 × 4–5 μ. Bresadola, however, considers it a reduced form of *O. pyxidata.*

The spores of our plants measure 6–7 (8, rarely 10) × 4–5 μ. The pileus and stem are "mikado brown" to "cinnamon-rufous" (R.) when fresh, fading to "cinnamon" or paler. The gills are broad, at first broadly adnate-decurrent, at length acuminately decurrent, subdistant, pallid. The stems measure 3–4 cm. × 1–2 (3) mm., and the pileus is 1–2.5 cm. broad. Cystidia none.

OMPHALIA LITUA Fr.–Ricken. — Our plants agree well with the figures of Fries (*Icones*) except that the stems are inclined to be slightly shorter. The spores measure 5–6 (8) × 2.5–3 μ. Cystidia none. In size and in the color of the pileus, gills and stem, it looks like *Clitocybe concava*, but the spores are much smaller, and the stem is rigid-cartilaginous.

OMPHALIA MAURA Fr. — This species is frequent in Oregon and Washington, preferring burned-over ground.

Omphalia nitrosa Kauff., sp. nov. — PILEUS 3–8 (rarely 15 or

20) mm. broad, membranous, subhemispherical, striate, snow white, glabrous, margin at first straight; flesh white. GILLS broadly adnate, slightly decurrent, broad, subdistant to distant, pure white, edge fimbriate. STEM 2–4 cm. long, 0.5 mm. thick, equal, filiform, entirely naked under lens, even, slightly tough, snow white, easily separating from the old fallen needles of Douglas fir on which they grow. SPORES elliptic-ovate, narrow, pointed at one end, hyaline, smooth, 7–8 × 3.5 μ; *cystidia* present, scattered on sides of gills, narrow, subfusiform, obtusely pointed, hyaline, 50–55 × 5–7 μ, more abundant and shorter and thicker on edge of gills. ODOR *nitrous* when plants are fresh, often unnoticeable in age.

Type collected on decaying needles of Douglas fir, by C. H. Kauffman, Takilma, Oregon, December 10, 1925.

This is distinguished from *O. gracillima* Fr.–Kauff., by its nitrous odor, the presence of cystidia, by the dried plants having assumed a clear rosy-incarnate hue, and by its habitat on conifer needles; perhaps also by the spores. Who can say what the spore size of *O. gracillima* is or what that species is? Ricken gives no spore measurements of his own; Rea (24) gives 11–12 × 4–5 μ; Bresadola (3), 7–9 × 2–3 μ; Saccardo, 6–7 × 3 μ. Kauffman (8) describes what he believes is the Friesian plant growing in frondose woods, and with spores 6–8 × 3–4 μ. The discrepancies are rather too great even in this genus, so that apparently *O. gracillima* is a composite species. The white, hemispherical, striate and glabrous pileus and the size are markedly the same for these two omphalias of the frondose and conifer habitat, respectively, but no author, to my knowledge, reports *O. gracillima* on conifer needles or growing in conifer forests.

OMPHALIA UMBELLIFERA Fr. forma OCHRALEUCA Kauff. (10).

Panus bacillisporus Kauff., sp. nov. — PILEUS 3–10(15) mm. broad, conchate or subspatulate to subreniform, thin, submembranous, pliant, subsessile or short stipitate, at first laterally extended then subresupinate, even, glabrous or minutely pubescent on margin, clay color or with slight rufous tint, margin pallid. GILLS decurrent, narrow, close, pallid, then with tint of incarnate. STEM, when present, 1–1.5 mm. long, lateral, 1 mm. thick, subpubescent, pallid or tinged rufous. SPORES minute, bacilliform, straight, 4 × 1–1.5 μ, hyaline; cystidia none; sterile cells not differentiated; basidia slender, 25–27 × 4 μ, 4-spored. ODOR and taste none.

Type collected on bark of fallen branches of Douglas fir, by C. H. Kauffman, Takilma, Oregon, December 5 and 8, 1925.

The trama of the pileus and gills is subgelatinous when examined under the microscope. The gill-trama is composed of compact parallel hyphae, its central axis loosening from the subhymenium and hymenium. The minute spores and the coniferous substratum are distinctive. It is gregarious. The species may belong to the section Resupinati of Pleurotus, considered by some (e.g. Murrill) as a genus because of the gelatinous characteristic. Externally the gelatinous character is not noticeable and the plants revive. It is scarcely possible that this can be a reduced form of *Panus betulinus* Pk. whose cap is fleshy and 5 cm. broad and which grows on birch in Newfoundland, although its spores are similar to those of our species.

PANUS STYPTICUS Fr. — On oak wood.

PHOLIOTA DISCOLOR Pk. — On logs.

PLEUROTUS SEROTINUS Fr. — On dead oak trunk.

PLUTEUS CALIFORNICUS McClatchie (*Proc. S. Cal. Acad.*, 1:384. 1897). — Since this species is incompletely described, an account of it follows:

PILEUS 1–2 (4) cm. broad, campanulate-expanded, obtuse, "dark olive" (R.) when young, soon "citrine-drab" or greenish-gray, subhygrophanous, with small radiating rugae, minutely pruinose-pubescent, dull, margin even or with short striae in age, at first incurved; flesh at first concolorous, then white. GILLS free, but at first appearing adnate, owing to the fact that the rounded truncated adjacent posterior edge lies close to the stem, becoming slightly remote, *broad*, ventricose, crowded, at very first pale citrine, at maturity "light ochraceous salmon" (R.), edge minutely fimbriate. STEM 2–5 (6) cm. long, 1.5–3 mm. thick, straight or curved, equal, "pale greenish yellow" (R.), glabrous, apex naked, solid, concolorous within. SPORES broadly elliptical to subglobose, 5–7.5 × 4.5–5.5 μ, slightly longer than wide, rounded at ends, smooth, pinkish in mass. CYSTIDIA scattered on sides and edge of gills, fusoid to slightly flask-shaped, apex obtuse, 70–75 × 16–22 μ, thin-walled, tinted with olive. ODOR and taste mild.

On very rotten mossy bark. The gill-trama is composed of convergent hyphae. The edge of the young gills may have an olive tint due to the colored cystidia. This species was described as having "irregular spores." In other respects, however, our plant is very much the same. *P. rugosodisca* Murr. from the East also seems exceedingly close.

PSILOCYBE OCHRAECEPS Kauff. (*Pap. Mich. Acad. Sci., Arts and Letters*, 5 : 143. 1925). — This species was common at Lake Quiniault, Washington, in the foothill forests, at Mt. Hood and at Takilma, Oregon.

RUSSULA CRENULATA Burl. (*Mycologia*, 5 : 310. 1913). — This species, although not frequent, is distributed throughout Washington and Oregon. The size of the pileus and stem varies considerably. The pileus is normally 4–7 cm., but may reach 9 cm. The stem is 4–7 cm. long × 5–12 (rarely 20) mm. thick. It is quickly very acrid. The gills and spores are white. The eastern counterpart is *R. albidula* Pk., which differs in the taste being tardily acrid in all parts, in its somewhat forked gills and more rigid and firm texture. The pellicle of the pileus of *R. crenulata* is separable from the disk, and the plants belong to the section Fragilis Fr., while *R. albidula* is one of the Rigidae, or at least close to that section, and the pellicle is adnate.

RUSSULA DELICA Fr.

RUSSULA DENSIFOLIA Secr.

RUSSULA EMETICA Fr.

Russula flava Romell var. **pacifica**, Kauff., var. nov. — This has so much the general appearance of *R. flava* that I am loath to separate it entirely. The taste is slowly subacrid, and the flesh does not, except indistinctly, show any cinerescent tendency. These are the characters of the variety. The spores are subellipsoid, with large oil drop, and measure about 7–8 (10) × 6–7 (8) μ, almost smooth under dry high powers of microscope, and are almost hyaline with a faintly tinted exospore. The gills are forked here and there at base only, at first white, then "straw yellow" to "Naples yellow." The pileus varies from "straw yellow" to "Naples yellow"; the stem is white or whitish. I have it from Montana, Washington and Oregon, where it occurs in coniferous forests, usually singly.

The type was collected at Takilma, Oregon, December 2, 1925. It differs from *R. ochraleuca* (Pers.) Fr. in the stems' not becoming ashy, although in advanced age they may become watery-grayish, but this occurs in other old Russula stems with otherwise unchanging flesh. Lange (17) says of *R. ochraleuca:* "It is generally said to be acrid, but in Denmark the almost insipid form is present, — in fact I have never met with really acrid specimens. Common in woods of Fagus. The spore powder is white." Evidently our plant is in some respects very similar to this species of Lange, but the gills and spores are not pure white, as in his, and the plant is more acrid.

RUSSULA GRANULATA Pk.

RUSSULA MAXIMA Burl. (*North Amer. Flora,* 9 : 229. 1915). — This species is well named because of its size. It was seen sparingly in Washington, Oregon and northern California. Its pileus is ordinarily 10–16 cm. or more broad, the stem 7–9 cm. long and very stout, 40–50 mm. thick. The gills are 10–13 mm. broad, mustard yellow or pale ochraceous when fresh. It grows solitary, a few scattered in a place, or a few in a cluster. In one collection the pileus had a "dark liver brown" (R.) color; ordinarily it has a "maroon" to "burnt-lake" (R.) color with an "ox blood-red" margin. The stem is usually intensely rose-colored. The taste is mild.

RUSSULA MURRILLII Burl. (*Mycologia,* 5 : 310. 1913). — The distribution of this species extends through Washington and Oregon to northern California. The color of the pileus varies, but is more often purplish rather than violaceous, as given in the description. The following paragraph gives the salient features.

Pileus 2.5–5 (6) cm. broad, "vernonia purple" (R.) to "dark vinaceous purple," rather firm, viscid, subpruinose when dry, short substriate on margin. Gills broadest in front close, scarcely subdistant, somewhat forked at base, white, at first, "buff yellow" (R.) at maturity. Stem 3–5 cm. long, 9–14 mm. thick, white. Taste mild. Odor none. Spores "buff yellow" in mass.

Russula Quéletii Fr.–Lange. — This name and *R. expallens* Gill., *R. sardonia* Ricken, *R. drimeia* Cke. and a few others are having a lively time by being continually shaken about, denied, accepted, argued about *ad infinitum,* as each succeeding author on the genus Russula gives his opinion. Our plants, rather frequently met with at Takilma, especially late, e.g. in December, had an "Indian red" button, which on expansion frequently remained Indian red on the disk, while the rest of the pileus and the stem took on shades of the Corinthian reds of Ridgway. The taste is acrid, although tardily at times. The gills are white at first then "straw yellow" to "cream color" (R.). The pellicle is adnate and only a narrow margin shows striae; it is viscid and shining. For all practical purposes this should have one of the names mentioned above. The purple red or dark purple pileus as shown in illustrations was not seen, at least under the weather condition that permitted occasional frosts. It occurred in the Douglas fir forest. The spores have a "cartridge-buff" color in mass. It was seen also at Lake Quiniault, Washington, in early November, under Douglas fir and smaller plants under thickets of Fatsia.

Russula veternosa Fr.

Stropharia ambigua (Pk.) Zeller

Stropharia fragilis Kauff.

Stropharia stercoraria Fr.

Stropharia sienna Kauff., sp. nov. — Pileus 4–8 cm. broad, fleshy, campanulate-expanded to almost plane, obtuse or obsoletely umbonate, center colored broadly with "burnt sienna" (R.), tawny olive or paler on margin, with a glutinous, toughish, separable pellicle when wet, at first with veil-remnants near margin, which is membranous and even;

flesh avellaneous, 2–4 mm. thick. GILLS adnate with decurrent tooth, becoming slightly decurrent in age, *broad,* narrowed in front, subventricose, close to crowded, "clay color" (R.), with fuscous tints when mature, edge entire, concolorous. STEM 5–7 cm. long, 5–8 mm. thick, rather slender, curved or flexuous, equal or only slightly enlarged at base, peronate by an appressed, fibrillose, rufescent-tinged veil to near the apex, with an evanescently fibrillose annulus, apex faintly yellowish, at first stuffed then hollow, whitish to faintly yellowish within. SPORES ellipsoid to oval (almost corn-kernel-shaped in one view), fuscous in mass, pale fuscous-purplish under microscope, smooth, 6–7 (8) × 4–5 μ. CYSTIDIA abundant on side and edge of gills, lanceolate, subventricose below, neck tapering to obtuse apex, hyaline, thin-walled, 60–65 × 9–16 μ; basidia short, 16–18 × 4–5 μ, 4-spored. ODOR *strong, penetrating,* Inocybe-like or *of iodoform.* TASTE tardily disagreeable.

Type collected by C. H. Kauffman, on the ground under oak and Douglas fir mixed with bushes, Takilma, Oregon, December 2, 1925.

This belongs in the subsection to which *S. aeruginosa* Fr. belongs. One might think it to be a discolored form of this species, since such are not uncommon. The size of the spores is the same also. It differs, however, from that species not only in color, but by the presence of lanceolate cystidia, a fibrillose sheath on the stem and a penetrating distinct odor; the stem is not viscid.

SCHIZOPHYLLUM COMMUNE Fr. — On Douglas fir.

TRICHOLOMA ALBOBRUNNEUM Fr.
TRICHOLOMA MELALEUCUM Fr.
TRICHOLOMA NUDUM Fr.
TRICHOLOMA RUTILANS Fr.
TRICHOLOMA SORDIDUM Fr.
TRICHOLOMA TERREUM Fr.

GASTEROMYCETES

ASTRAEUS GIGANTEUS Lloyd. — On the ground in mixed woods.

ASTRAEUS HYGROMETRICUS (Pers.) Morg. — On gravelly soil under white oaks. (Same as *Geaster hygrometricus.*)

BOVISTA PILA B. & C.— In a barnyard.

BOVISTA PLUMBEA (Pers.) Fr. — In open grassy places.

CRUCIBULUM VULGARE Tul. — On cow dung.

GEASTER TRIPLEX Jungh. — In mixed woods.

LYCOPERDON ATROPURPUREUM Vitt. var. FLOCCOSUM Berk. — Under fir and oak.

LYCOPERDON CEPAEFORME Bull. — Along woods. Perhaps only a form of *L. polymorphum* Vitt.

LYCOPERDON GEMMATUM Batsch. — Under fir and oak.

LYCOPERDON SUBPRATENSE Lloyd. — In open grassy places. This is close to *L. pratense* Pers. of Europe, according to Lloyd.

NIDULA MICROCARPA Pk. — On wood.

NIDULARIA PISIFORMIS (Roth) Zeller. — On old canvas rotting on the ground.

RHIZOPOGON LUTEOLUM Fr. & Nordholm. — Under conifers.

RHIZOPOGON OCCIDENTALIS Zeller & Dodge. — Frequent. Under conifers.

SPHAEROBOLUS STELLATUS Tode. — On cow dung.

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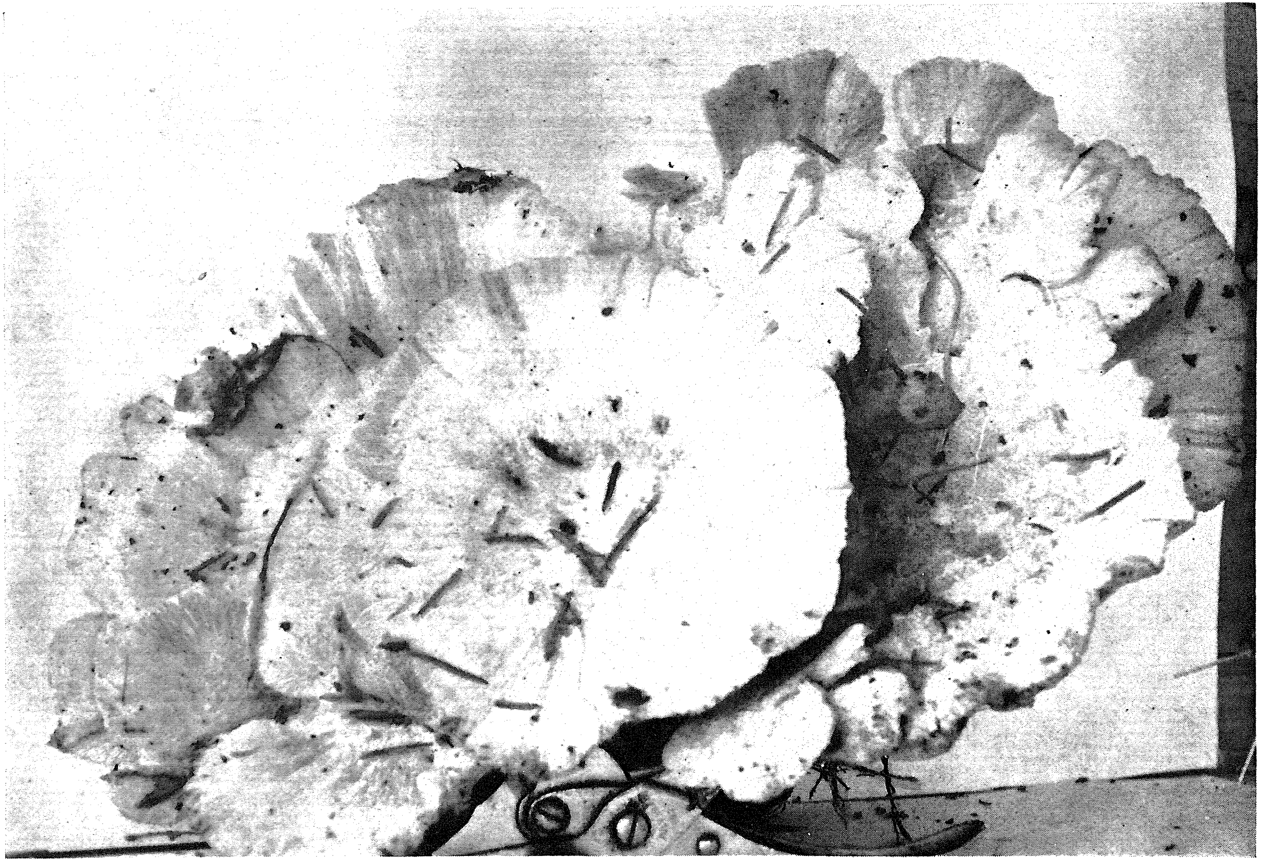
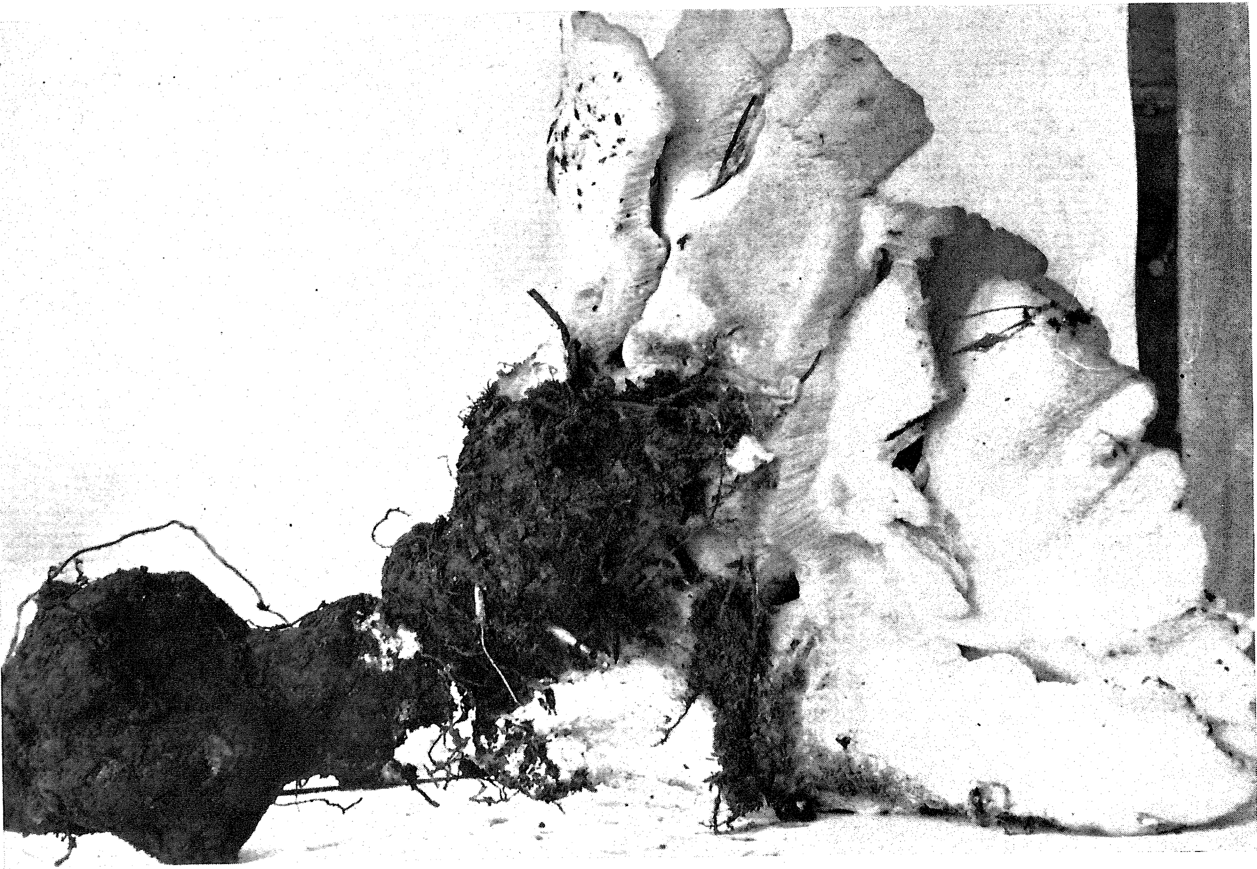
PLATE XXIV



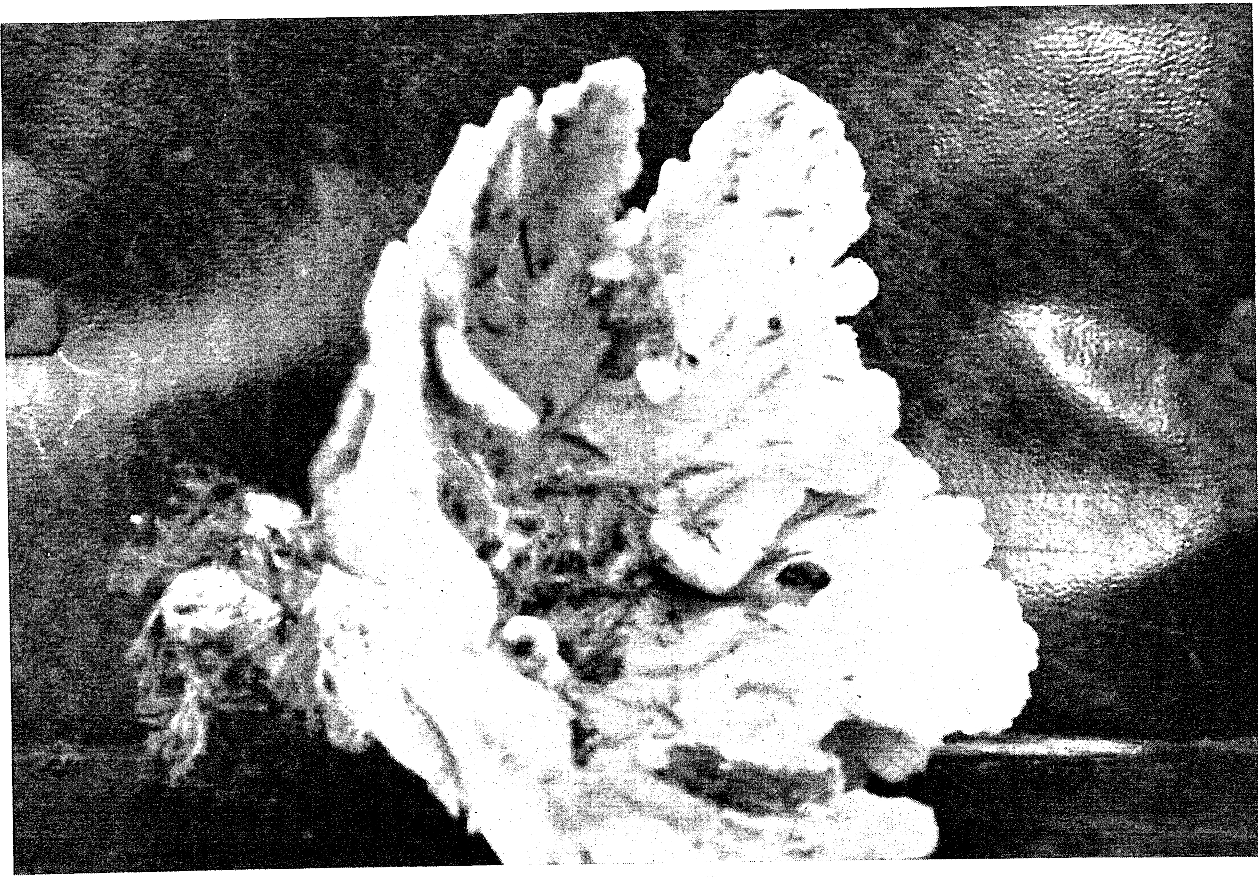
Polyporus pacificus Kauff., sp. nov.
(Reduced one half)

PLATE XXV



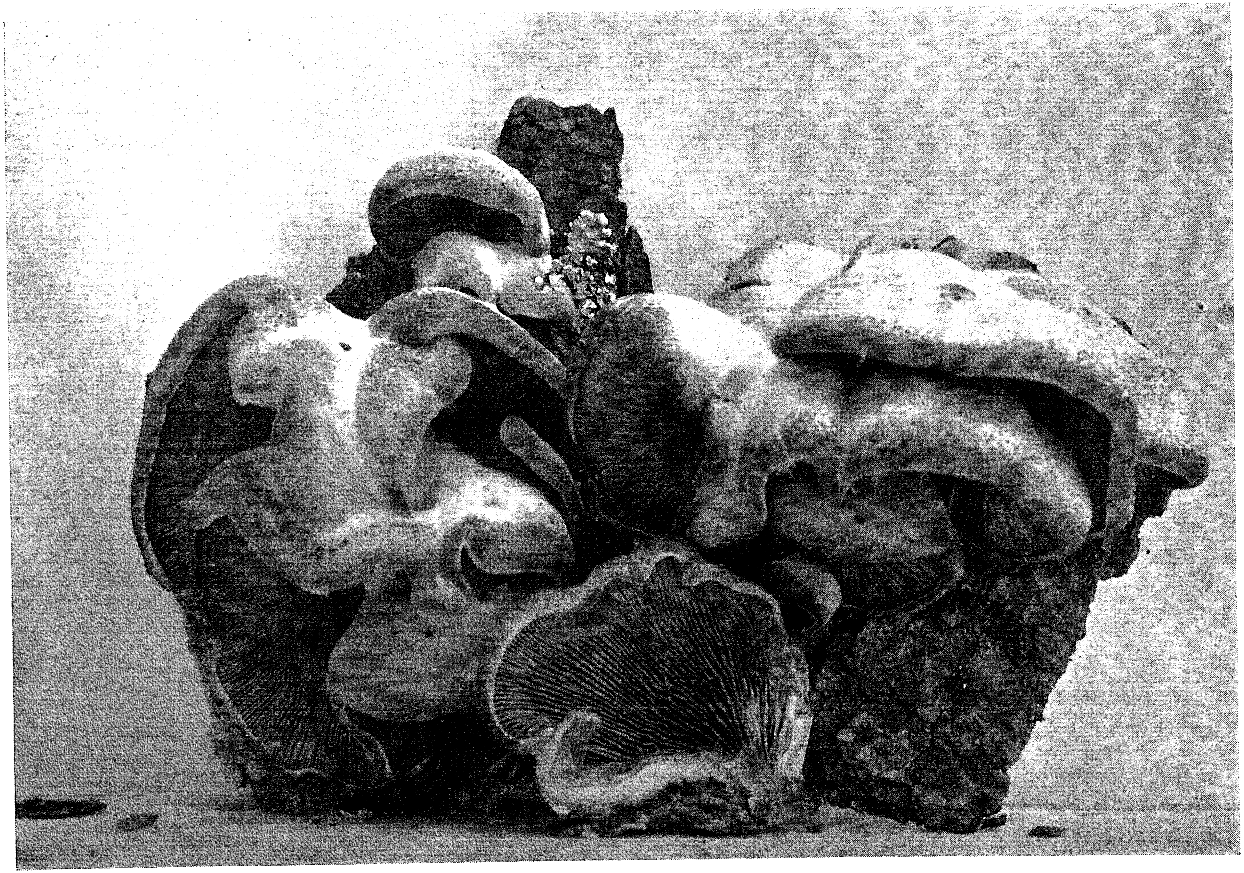
Polyporus pacificus Kauff., sp. nov.
(Reduced one half)

PLATE XXVI



Polyporus pacificus Kauff., sp. nov.
(Reduced one half)

PLATE XXVII



Claudopus nidulans Fr.

ECOLOGICAL NOTES ON KALAMAZOO COUNTY, MICHIGAN, BASED ON THE ORIGINAL LAND SURVEY

LESLIE A. KENOYER

KALAMAZOO COUNTY, in southwestern Michigan, is entirely covered with glacial drift. According to Leverett,[1] two well-marked terminal moraines extend almost across the county from northeast to southwest, one on the eastern and one on the western side. An extensive ground moraine enters the county on the southeast, and a smaller one on the southwest corner. Aside from a little lake clay which indents the north boundary near the northwest corner, the remainder of the county, embracing almost two thirds of its area, is indicated as outwash plain. The vegetation is almost entirely deciduous forest, with both the beech-maple and the oak-hickory types well represented.

In many spots over the county there remain small woodlots which give one a general idea of the former distribution of forest types. But so much of the area has lost all trace of its original cover that boundaries are somewhat uncertain. Prompted by a desire to secure a picture of this original cover, I looked up the old land survey records and found a book of field-notes based upon the original survey. In this book each section corner and the middle point of each side of each section are located with reference to two "bearing trees"; their species, their diameter and their direction and distance from the stake are stated. This survey was made from 1826 to 1830, when the site of the present city of Kalamazoo was occupied by the Matchebenashewish Indian Reservation. The first white settler arrived in the county in 1828.

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[1] Leverett, Frank. Map of the surface formations of the Southern Peninsula of Michigan. Michigan Department of Conservation. 1924.

The plotting of these bearing trees on the county map helps one to judge with considerable accuracy the original limits of the four important plant associations: beech-maple forest, oak-hickory forest, swamp forest and prairie. These limits are shown on the accompanying map (Map 3). There are approximately 576 square miles in the county. About one fourth of this area, or 140 square miles, was beech-maple forest; about 36 square miles, prairie; about 20 square miles, lakes and their surrounding aquatic zones; probably 50 square miles, swamp and stream bank forest; and the remainder, rather more than half of the county, oak-hickory forest.

The prairie areas were settled early, since they consisted of very rich land that did not require much clearing to fit it for cultivation. Their location is easily defined from the field-notes, for the corner is described as a stake in the prairie, or its bearing is defined with reference to one or more bur oak trees which are generally some distance, sometimes several chains, away from the stake. Schoolcraft, Climax, Richland, Galesburg and part of Kalamazoo were established on these open areas. So thoroughly have they been cultivated that most traces of the original vegetation have disappeared. Prairie species once occurring in the county are no longer to be found. The prairies are all on glacial outwash, level in contour and on soil of high organic content. It is believed that they began as marshes. Even now around the borders of lakes are wet meadows that show the transition from marsh to prairie.

The beech-maple areas constituted the most dense and the most picturesque woodlands. There are four fair-sized areas and several smaller ones. Two of the latter, those of the southeastern and southwestern corners of the county, are practically limited to the rich ground moraine, while the other two occupy partly terminal moraine and partly glacial outwash. Most of the beech-maple association is on soil classified by McCool and Veatch[2] as medium in organic matter (2 to 4 per cent), but about 16 square miles of the 140 of beech-maple in the county occupy soil tabu-

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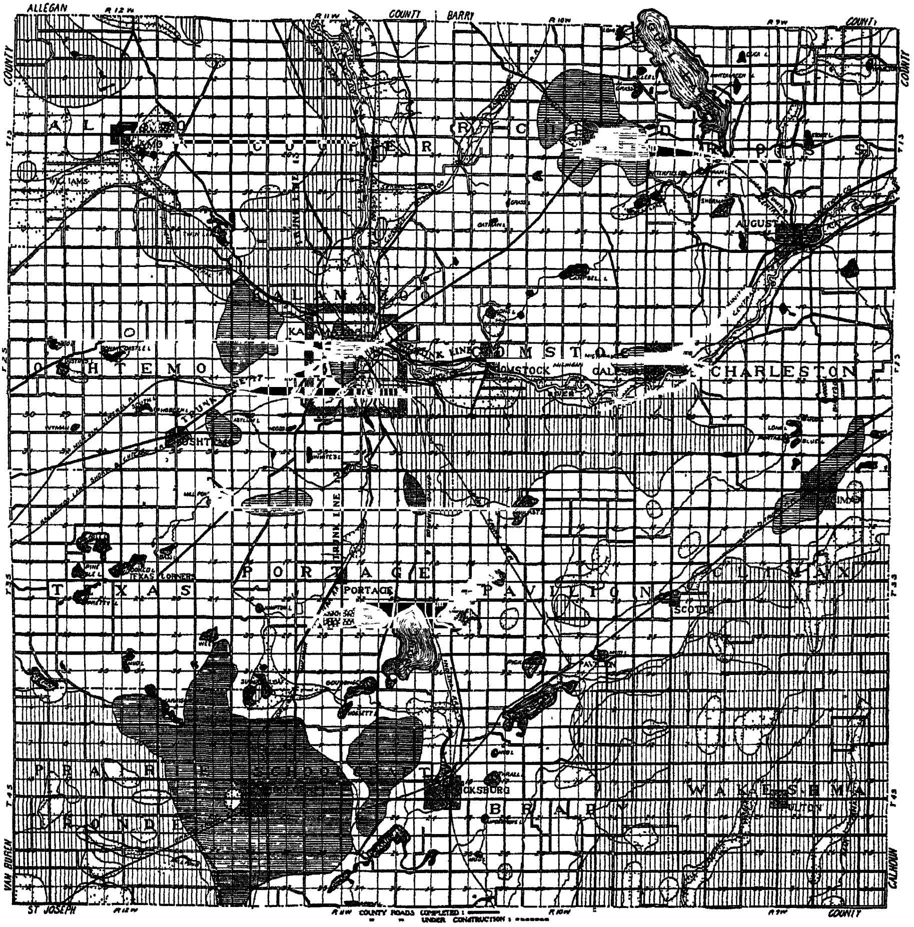
[2] McCool, M. M., and Veatch, J. O., *Organic Matter in Kalamazoo County Soils*. Mich. Agric. Exper. Sta. Circular Bull. No. 110. 1929.



Map 3. Map of Kalamazoo County, Michigan, indicating the original plant associations as determined from the field notes of the old land survey
Unshaded area, oak-hickory forest
Vertically shaded area, beech-maple forest
Stippled area, swamp forest, including stream bottom forest
Horizontally shaded area, grasslands, with scattered bur oak

lated as low in organic matter (less than 2 per cent). The fairly level character of most of the beech-maple area and the good quality of the soil have caused this formation to suffer more from cultural influences than has either of the other forest types. It is a type which southern Michigan is in danger of losing, and which should be included more extensively in projects for parks or reserves.

Oak-hickory forest covers considerably more than half of both the terminal moraine and the outwash. It occupies nearly all the land mapped by McCool and Veatch as low in organic matter, and a good many square miles of the land indicated as medium in organic matter, mostly along the edges of the areas so indicated. Beech-maple seems to occupy the more mature topographies and oak-hickory the younger ones. Wakeshima Township is the only one in the county that does not contain at least a portion of a lake, and it is the only one that is completely covered with beech-maple. Oshtemo is the only township that has no streams large enough to show on the map, and it is almost entirely oak-hickory. Further research should throw more light on the edaphic and climatic conditions that swing the balance toward beech or toward oak.

A careful checking up of the forest remnants now standing indicates that almost without exception the boundaries of the associations remain where they were a century ago. Intensive work was done along the border lines of the areas, where succession, if sufficiently rapid, should be evident, and with surprising exactness the remnants of today fit the forests of a century ago.

If beech-maple were succeeding oak-hickory under the relatively undisturbed conditions existing at the time of the survey, the fact might be revealed by a comparison of the beech trees along the borders of a beech-maple area with those in the center of the same area as regards size and density of stand. The former might be expected to be smaller, or to be farther apart, than the latter. From the edge of the largest beech-maple area 27 reference trees were taken, all of them within half a mile of the bordering oak-hickory forest. From the interior of the same area, far removed from any oak, 37 trees were taken. The former average 11 inches in diameter and 27 links from the stake; the latter, 10.8 inches in diameter and 20.8 links distant. The difference seems too slight to be significant.

In just a few of the present woodlots may be seen young beech trees in groves of large oak trees. The unprecedented cultural conditions of the last century may have interfered with the natural progress of succession. But the evidence at hand would suggest that succession, if occurring, is very slow, or that possibly the oak-hickory and the beech-maple might be regarded as edaphic climaxes which under present climatic conditions are just holding their own.

Swamp forest, as here considered, includes tamarack, which is frequent about lakes and along sluggish streams, the forest of yellow birch, red maple, black ash and swamp oaks, which occur on somewhat higher and drier ground, and the forest of elm, silver maple, sycamore and honey locust which is found along streams. Perhaps the stream-bottom forest and the lake-swamp forest deserve separate recognition, but from the data available it is not easy to separate them. The swamp forest is generally regarded as transient. Birch, red maple and ash follow tamarack, and these in turn are followed by beech and maple or by oak and hickory, depending on which type is near enough at hand to seed the ground. But in the past century there has been no striking replacement of the swamp type, even though the draining of marshes might be expected to hasten somewhat the ordinary course of succession.

Pines were then, as now, very sparsely represented in the area, not more than two in the entire county being used as reference trees.

If we were to assume that the two trees selected as reference trees were always the two trees of fair diameter nearest the stake, the frequence of the different species on the list of reference trees would be an index to their frequence in the county as a whole. Counting only the trees at the quarter section corners, and disregarding those on the intersection of the surveyor's line with river and lake borders and with the boundaries of the Indian reservation, one finds the ten species most frequently used, together with the number of times, are as follows:

White oak	1571
Beech	493
Bur oak	309
Yellow oak	175
Tamarack	108
Elm (species not designated)	102
Sugar maple	99
Black ash	76
Hickory (species not designated)	71
White ash	51

Thirty-one species were used, but some of them only a small number of times. The plotting of these species in the order of their decreasing frequence gives a curve of the hyperbolic type, with a decrease in successive numbers of individuals very rapid at first, but becoming less and less as the curve flattens out on species with only one representative. I believe this is a rather general law for the distribution of organisms. It agrees remarkably with the findings of Raunkiaer,[3] who noted that, if a series of small sample plots are taken at random in any uniform association, many species are represented on less than one fifth of the whole number of plots, while only a few, often but one or two, are represented on more than four fifths.

It is of interest to note that beech was used about five times as frequently as was sugar maple, whereas most of the woodlots now remaining show maple rather more plentiful than beech. It has been suggested to me that, because of its smooth and easily marked bark, beech was chosen in preference to other trees. If this is true, the average diameter of the beech trees used should be less or else their average distance from the stake should be greater than the diameter and distance of the sugar maple trees that were used. To a slight degree this seems to be true. For example, in Wakeshima Township there were used for reference 137 beech trees 10.5 inches in diameter and 23.2 links from the stake, also 36 maple trees 13.8 inches in diameter and 20.1 links distant. In Climax Township there were employed 72 beech trees 11.2 inches in diameter and 22.7 links distant, and 18 maple trees 12.1 inches in diameter and 21.7 links distant. The difference is so slight as to show comparatively little selective preference for beech, and to suggest that, in relation to maple, beech was more numerous than it is in most places today. It is also remarkable that white oak was nine times as much used as yellow oak, which seems to rival it in abundance now.

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[3] See article by the writer in *Ecology*, 8 : 341–349. 1927.

I believe that the sizes and distances of the reference trees can be used in constructing a picture of the size of the trees and the density of the forests of that time. To secure data for comparison of the present forests with the original, two trees were selected near each of a number of points taken at equal intervals in one of our best beech-maple woodlots of today. The average diameter and distance of the two nearest large trees are approximately what they were in the beech-maple areas at the time of the survey. But beech seemed rather less plentiful with reference to other trees than it was in the survey. Several oak-hickory groves similarly investigated seem much more dense than the average of the oak-hickory area at the time of the survey. This would indicate that much of the oak-hickory area was not occupied by real timber, but by sparsely scattered trees. The same conclusion may be reached by a comparison of the oaks of the survey with the beeches. Calculating from the data for several townships, one finds that the average beech was about 11 inches in diameter and 24 links from the stake, while the average white oak was slightly larger (13.5 inches in diameter), but was much farther from the stake — 77 links. If we square the distances for a comparison of the density of stand, it seems that the beech area averaged approximately nine times as dense as the oak. On the whole, it seems fair to assume that the well-preserved woodlot of the present is not inferior in size and density to the forests at the beginning of settlement.

Data similar to those used for Kalamazoo County are doubtless obtainable for the other counties of the state. The analysis of vegetation by their use seems a project quite worth while. The writer will welcome any suggestions bearing on the proper interpretation and use of such material.

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SOME CHIMERAS OF *SOLANUM TUBEROSUM* L. *

JOHN ERNEST KOTILA

POTATO growers occasionally report the discovery in their fields of a few tubers which are strikingly different from the normal character of the tubers of the variety being grown. Frequently these "off type" tubers are found to be the result of accidental mixing of varieties. Occasionally, however, they are reported by farmers who grow but a single variety of potatoes and their presence can hardly be explained in this manner. Bud sports or somatic mutations in potatoes have been reported by a number of investigators and T. Asseyeva (1) has shown them to be in the nature of periclinal chimeras.

Potato varieties are not in general considered to be "pure lines," but rather mixtures of clons, and the bud mutations which have been reported from time to time were discovered in fields which evidently were planted with such mixtures. Several of the chimeras reported in this paper were found in similar fields; the others were discovered in clons which originated from single tubers selected by the writer in 1922, and which have been increased each year since that time under his supervision.

CHIMERAS IN MIXED CLONS

Russet Rural — fasciation

A chimera was collected in 1927 in a field of Russet Rural potatoes by Mr. P. R. Biebisheimer, an inspector for the Potato Certification Service of the Michigan Crop Improvement Association. His attention was attracted to the plant because of its fasciated stem. It appeared as though three stems were joined

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* Published as Michigan Agricultural Experiment Station Journal Article No. 9, N. S.

together. Except for this abnormality the plant appeared to be typical for the Russet Rural variety. The largest tuber produced by this plant was selected by the writer to determine whether this abnormality was carried in the tuber and transmitted to the next vegetative generation. Six one-eye pieces were cut from the tuber and planted during March, 1928, in separate pots in the greenhouse. A sprout emerging from one of the eyes was observed to be fasciated. One cutting failed to grow, but all the others produced plants with fasciated stems. The fasciation, however, with one exception, instead of beginning at the seed piece as occurred in the field, was not produced until after three or more nodes had been formed. The stems below the fasciation appeared to be normal. One of the three sprouts produced by the eye in which a fasciated bud was observed proved to be the exception and in this the entire stem was fasciated. The fasciation in the other two stems occurred at the fifth and seventh nodes. The tubers produced by this cutting were saved for further observation, and after the dormant period all the eyes of one of these tubers showed fasciated sprouts; the sprouts of the other tubers were apparently normal (Pl. XXVIII). Evidently this chimera is transmitted through tubers from one vegetative generation to the next.

Green Mountain — "spinach leaf"

A chimera occurs quite frequently in this variety which is characterized by the laminae of the leaflets of some of the bottom leaves being joined together, giving them the appearance of spinach leaves; hence this aberration has been designated as "spinach leaf." It has been observed on plants of various other varieties, including Bliss Triumph, Irish Cobbler and some of the varieties of the Rural group. This abnormality sometimes causes a stunting or retardation of the growth of the affected plants.

In the summer of 1928 in the course of observations in a field of Green Mountain potatoes in which an unusually high percentage of the plants showed the "spinach leaf" chimera, one plant was found which, in addition to having this abnormality, possessed abnormal blossoms also. The corollas of these were green instead of white, which is the normal color for Green Mountain blossoms.

Single-eye cuttings made from the tubers formed by this plant when grown in the greenhouse during the winter of 1928–29 produced plants all of which had some abnormal leaves like the parent plant. Unfortunately, conditions in the greenhouse were not favorable for bringing the plants into blossom, so that it could not be determined whether the green corolla character was carried over in the tubers also.

CHIMERAS IN SINGLE TUBER CLONS

Bliss Triumph — white and variegated tubers

During the 1926 potato harvest a white-skinned tuber was discovered in a single-tuber clon of Bliss Triumphs, the normal skin color of which is red. The eyes of this tuber were red and showed that it was a chimera of the Bliss Triumph variety and not an admixture of the Irish Cobbler variety, the tubers of which have somewhat the same type as the Triumph, but which are white-skinned. This tuber and its vegetative progeny have been grown for four vegetative generations and the resulting tubers have been white like the parent chimera discovered in 1926. The vine growth of these plants has been normal for the Bliss Triumph variety.

The discovery of the white chimera in 1926 led to the making of careful observations during the 1927 harvest, with the result that six aberrant tubers were found in various Bliss Triumph single-tuber clons. Some of these tubers were variegated, being partly red- and partly white-skinned, and others were entirely white except for small splashes of red (Plate XXIX). The eyes of all tubers were red. During the 1928 winter the eyes of each tuber were planted in separate pots in the greenhouse and the progenies of these plants were grown in the field during the following summer. The behavior of these single-tuber clon chimeras is shown in the table on page 222.

DISCUSSION

It will be noted from this table that with one exception the eyes from the red portions of the tubers produced plants which formed red tubers and the eyes from the white portions produced plants which formed white tubers. The exception was eye No. 4 of

TABLE I

Behavior of Bliss Triumph Single-Tuber Clon Chimeras for Two Vegetative Generations

Clon No.	Tuber No.	Appearance of tuber	Eye No.	Color of eye region	Behavior	
					Generation 1 Color of tubers	Generation 2 Color of tubers
179	862	Variegated red and white	1	Red	3 Red	Red
			2	Red	3 Red	Red
			3	Red	6 Red	Red
			4	White	3 Red	Red
179	863*	Variegated red and white	1	Red	6 Red	Red
			2	Red	4 Red	Red
			3	Border	5 White	White
			4	Border	6 Red	Red
179	864†	Variegated white and red	1	White	3 White	White
			2	White	6 White	24 white, 1 red
			3	Border	5 Red	Red
			4	Border	4 Red	Red
179	865	White	1	White	3 White	White
			2	White	4 White	White
			3	White	5 White	White
178	866	Variegated red and white		Planted whole	3 Red	Red
246	867	White	1	White	5 White	White
			2	White	5 White	White

* See Plate XXX. † See Plates XXXI–XXXII.

tuber No. 862, taken from the area blotched with white which occurred on that tuber. The white area on this tuber was not as clearly defined as in the other variegated tubers and a tapering projection of red skin extended from the eye to the normal portion of the tuber. The production of red tubers by this cutting may have resulted because the buds were normal in spite of the fact that the eye was almost completely surrounded by the white area.

Those eyes which were on the line dividing the red from the white areas yielded interesting results. Some of these produced white tubers and others formed red ones; the color of the tubers produced probably depended upon whether the dominant bud arose from the red- or the white-skinned portion of the eye.

The apical eyes of a potato tuber are known to be dominant over the lateral ones and are the first to develop after the dormant period of the tuber. The variegated tuber No. 866, which was planted without cutting, no doubt produced red tubers because the plant which ensued arose from a dominant apical eye, which occurred in the red area of the tuber.

The behavior of the second vegetative generation of the 1927 chimeras was like that of the 1926 chimera and the tubers which were produced were like those which were planted, with one exception. Tuber No. 5, produced by eye No. 2, which occurred in the white portion of the variegated tuber No. 864, yielded three white tubers and one red tuber. Evidently a reversion had occurred in the bud which produced the stolon upon which this tuber was formed, which permitted the development of a normal red-skinned tuber.

Phenomena such as those reported above are of more than casual scientific interest and some potato chimeras may have considerable economic significance, as is shown, for example, by the Russet Rural variety of potatoes. This variety, because of its disease-, insect- and drought-resistant qualities, is the standard late variety most extensively planted by growers of certified seed in Michigan, and hundreds of carloads of Russet Rural seed potatoes are shipped annually to potato growers in other states. The occurrence of the chimeras discussed above lends confirmation to the account given by Mr. George Priestley, of Kalkaska, Michigan, of his discovery of the Russet Rural potato in 1903. Mr. Priestley related that he found russeted tubers to the number of seventeen in various parts of his field of Rural New Yorkers, and that he usually found one or two tubers of this type in a hill, the other tubers being normal white-skinned Rural New Yorker tubers. From Mr. Priestley's story it would seem that the Russet Rural variety arose as a russet-skinned chimera of the Rural New Yorker. Some support for this is found in the fact that very often Russet Rural tubers are found which are not entirely russeted, but show smooth-skinned areas intermingled with the russeted areas. Further evidence of the chimerical nature of this variety was obtained during the 1928 season when two hills were found in a Russet Rural single-tuber clon, grown under conditions to preclude any mixing of material, which produced white, smooth-skinned tubers. Experiments are now under way to determine definitely whether the Russet Rural is a chimera of the Rural New Yorker, and in this work the method described by Asseyeva (1) is being followed.

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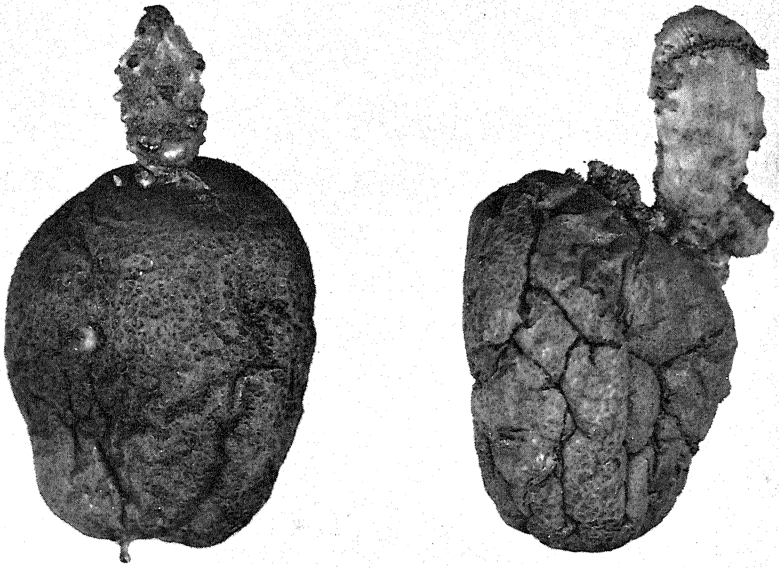
LITERATURE CITED

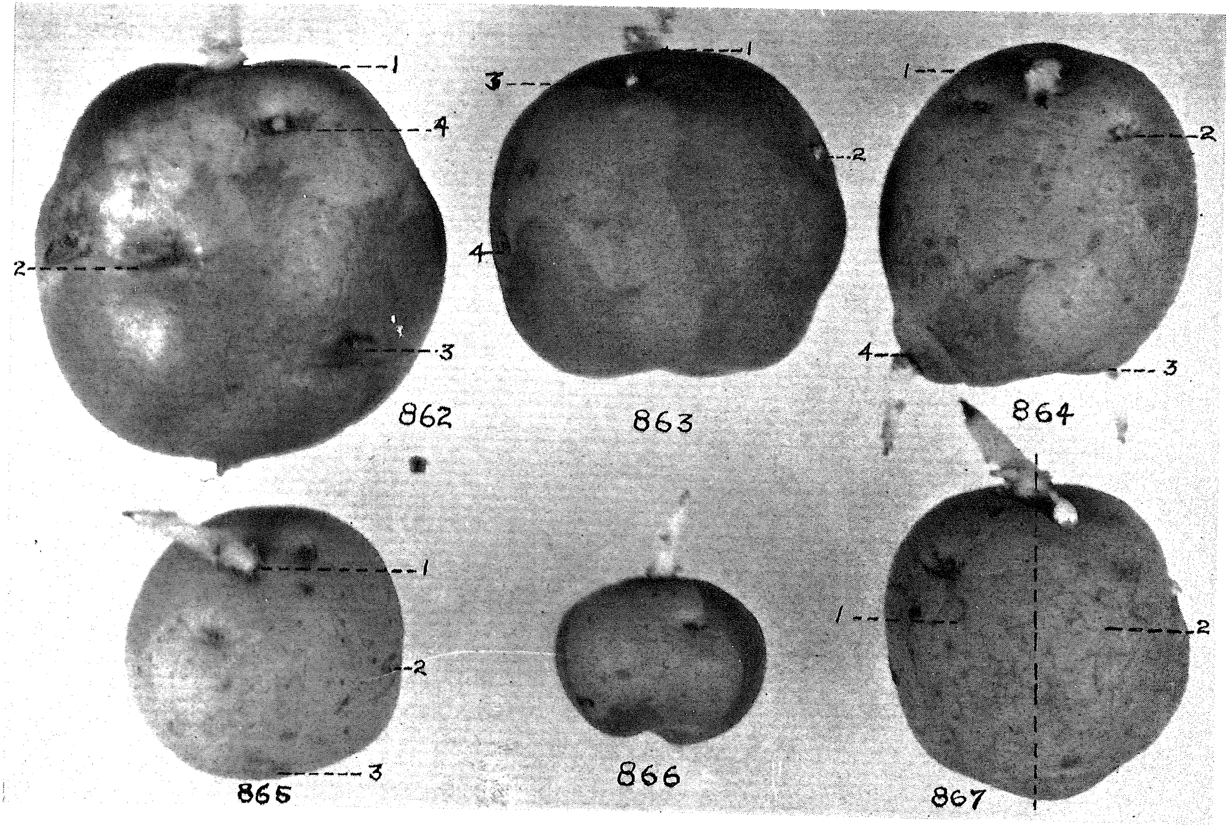
ASSEYEVA, T. 1927. Bud Mutations in the Potato and Their Chimerical Nature. Journ. Gen., 19 : 1–26, pl. 1, figs. 7.

PLATE XXVIII



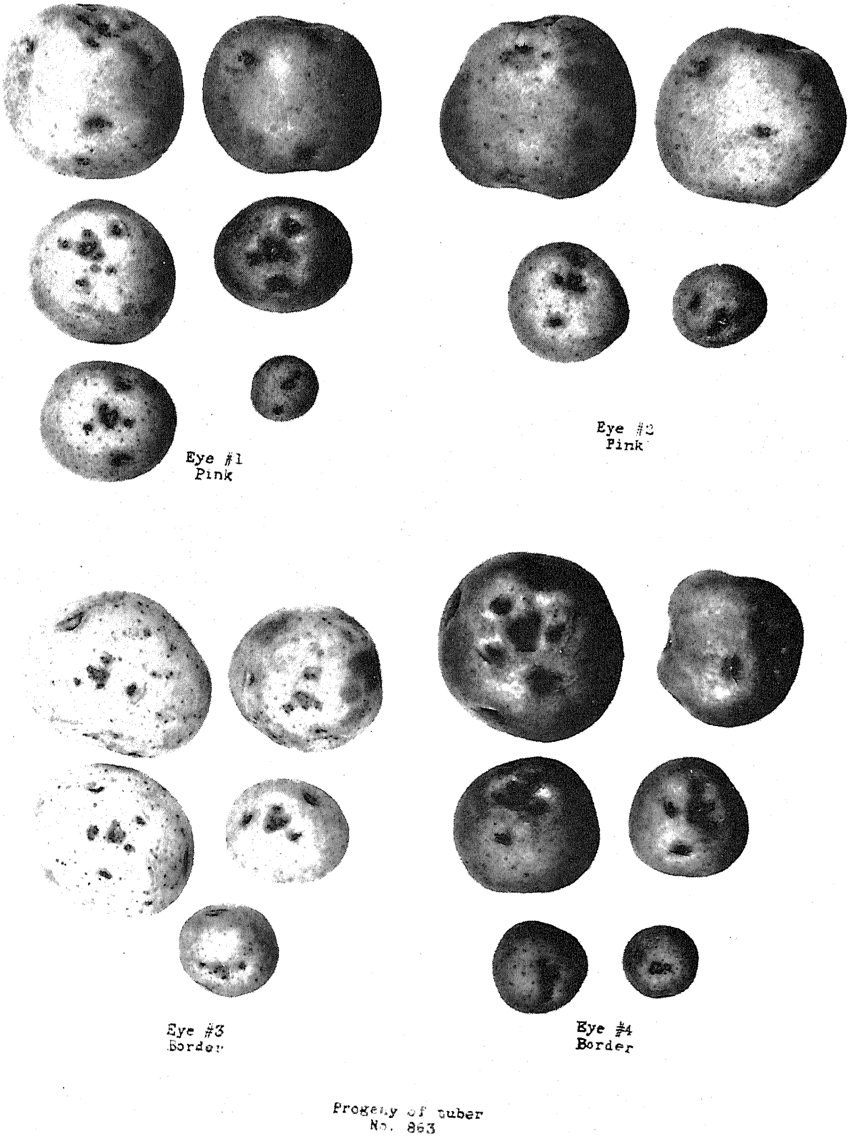
Tubers produced by Russet Rural fasciated stem chimera. Note fasciated sprouts produced by the tuber at the right

PLATE XXIX



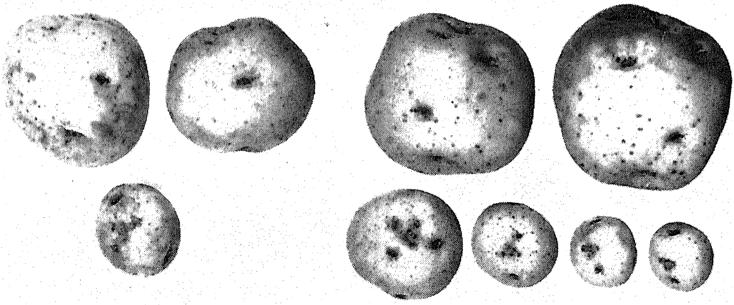
Chimeras discovered in Bliss Triumph single tuber clons in 1927

PLATE XXX



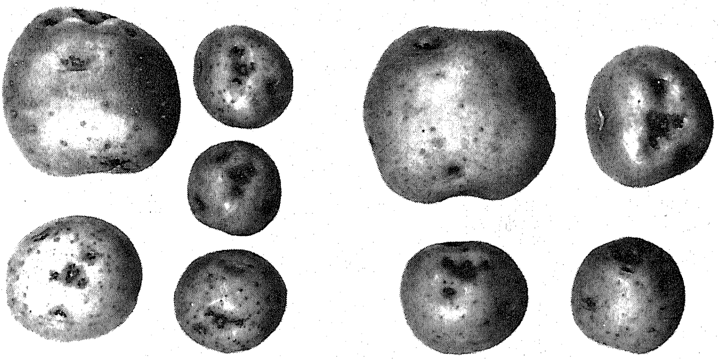
First generation progeny of eyes of tuber No. 863. See Plate XXIX. One border eye produced white tubers; the other, red ones

PLATE XXXI



Eye #1
White

Eye #2
White



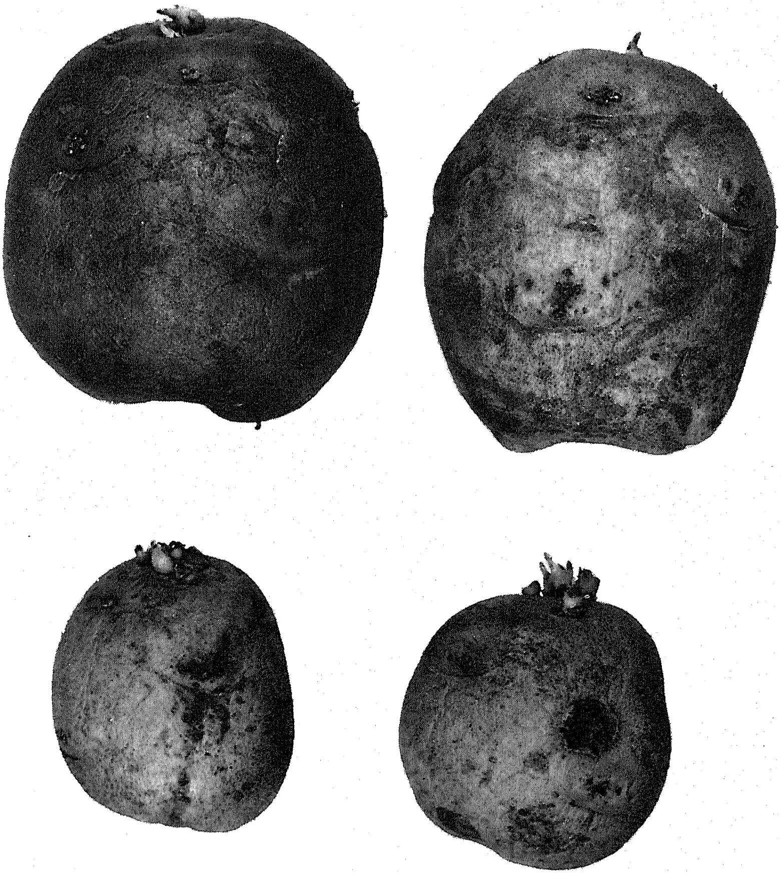
Eye #3
Border

Eye #4
Border

Progeny of tuber
No. 864

First generation progeny of eyes of tuber No. 864. See Plate XXIX. Both border eyes produced red tubers

PLATE XXXII



Second generation progeny of tuber No. 5, eye No. 2, tuber No. 864. See Plates XXIX and XXXI. One red tuber in the hill, others white

REGENERATION IN SOME AMERICAN MOSSES *

CARL D. LA RUE

THOUGH extensive studies have been made on the regeneration and growth in culture of European mosses by Correns (2), Heald (3), the Marchals (5–7), Servettaz (10), Westerdijk (12), Wettstein (13) and others, little has been done with American species.

The writer became interested in the classic work of the Marchals and the more recent investigations by Wettstein and desired to make similar studies on local species. It seemed particularly desirable to know to what extent such species could be regenerated and grown in controlled cultures. This report embodies the results of his observations and investigations on both gametophytic and sporophytic tissues of these mosses.

GAMETOPHYTIC REGENERATION

Methods of culture

The emphasis in these tests was put on the possibility of growing these mosses in culture and on securing regeneration from the different organs. Therefore, no special physiological study was made. Heald (3) has shown that the development of protonemata and of buds takes place most readily in light. Consequently all the cultures were kept in the light. Robinove and La Rue (9) have shown that mosses are usually not particular as regards the

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* Paper from the Department of Botany of the University of Michigan, No. 314. A part of the work reported here was done at the University of Michigan Biological Station.

This investigation was aided by a grant of funds from the Society of the Sigma Xi.

hydrogen-ion concentration of their substrata, and accordingly no tests of this environmental factor seemed necessary.

In the beginning the Marchal solution was used as a nutrient, but later Benecke's solution as used by Wettstein (13) was employed. Cultures were tried with the Marchal solution in sand and on filter paper saturated with the Marchal solution. These usually gave results inferior to those in which the plant parts were floated in the solution, so the results recorded here are those gained by the latter method.

The mosses were not sterilized in any way, but were washed carefully with sterile distilled water before they were put into the culture solution. Since the solution does not contain sugar, no trouble arose from bacterial or fungous contamination. The cultures were made in Syracuse watch glasses which were stacked up in the usual fashion. This, of course, meant that the light received by the plants was rather weak. The cultures were kept in a west window and were shaded from direct sunlight.

Benecke's solution was used in almost all the tests in agar on which the leaf and stem segments were laid. The agar was poured in petri dishes and sterilized. Some contamination of the agar was inevitable when the plants were placed on it, and bacteria and fungi frequently developed. Usually these growths were not injurious to the rapid growth of the protonemata and it is certain that none of the failures of regeneration of any species were due to contamination. Green and blue green algae were also rather troublesome contaminations, especially in cultures in which the plants were slow to regenerate, but it is quite certain that these cannot be blamed for the failures reported. In all cases failures were observed also in cultures free from serious contamination.

No attempt is made here to be certain of the exact designation of the first outgrowths to appear on stems or leaves. Servettaz (10), Westerdijk (12) and Heald (3) all define rhizoids and protonemata according to their own conceptions. In most cases the first outgrowths observed in these cultures were clearly protonematal, but a few were doubtful. Some cultures gave mixtures of protonemata and rhizoids.

Most of the species tried on either nutrient medium regenerated readily. When they were tried on both media the results were usually the same and when that is so the species is listed in only one group. Considerable variation in the rate of regeneration, as well as in the type of regeneration, was found.

Results with the Marchal solution

In the following list the forms marked with an asterisk (*) have never before been regenerated or grown in culture.

Aulocomnium palustre (L.) Schwaegr. — This moss regenerates very readily. Pieces of the main stem and of gemma-bearing branches produce protonemata in five days. Detached leaves are of slower growth, but develop abundant protonematal outgrowths in nine days.

* *Calliergon cordifolium* (Hedw.) Kind. — Short stem segments develop rhizoids all along the sides, but not from the ends. Segments cut from the larger stems regenerate sooner than those from the smaller ones. Protonemata are developed by the leaves mostly at the tips, though some leaves show them at the base only.

* *Calliergon giganteum* Schimp. — This species behaves like the preceding.

* *Dicranum flagellare* (Hedw.) —As might be expected from the fact that the genus Dicranum contains several species which have special devices for vegetative reproduction, all the species tried save *D. montanum* were very active in regeneration. *D. flagellare* produces protonemata more readily than any other moss tested in these studies. The flagellate branches, which break off at a touch, are the natural means of vegetative reproduction, and throw out protonematal outgrowths in the Marchal solution within five days. Stem segments regenerate also, but a day or two later than the flagellate branches. Leaves detached from stems do not regenerate, but leaves attached to a stem segment even a millimeter long produce protonemata from their margins.

* *Dicranum scoparium* (L.) Hedw. — This species regenerates beautifully in from ten to twelve days. The stem is normally thickly clothed with rhizoids, but in spite of this new outgrowths are produced between these when the stem is cut into segments

and placed in the Marchal solution. Detached leaves regenerate, but pieces of leaf develop protonemata sooner than do whole leaves. Leaves attached to stem segments regenerate as well as detached ones.

* *Dicranum undulatum* Ehrh. — Stem segments regenerate very readily in ten days. Protonemata are produced at both tips and bases of leaves and pieces of leaves attached to stem segments. Detached leaves do not show any vegetative growth.

* *Dicranum viride* (Sull. Lesq.) Lindb. — The tips of the leaves of this species break off very readily and are supposed to be a natural means of vegetative reproduction. In culture these small tips did not regenerate, but larger pieces of leaf and detached whole leaves regenerated protonemata at their bases in nine days. Stem segments developed outgrowths at the bases.

* *Drepanocladus aduncus* (L.) Warnst. — The leaves of this species do not regenerate either when detached or when left attached to stem segments. Stem segments produce outgrowths along the sides when they lie in a horizontal position.

Fissidens adiantioides (L.) Hedw. — Leaves of this species do not regenerate at all in the Marchal solution. When the tips of the stems are cut off, they produce protonematal outgrowths from their apices, but not from the base. Some outgrowths are produced also along the ventral surface of stem segments lying in a horizontal position.

* *Hylocomiun splendens* (Hedw.) Br. & Sch. — This moss has a very characteristic growth habit in nature. The main stems are more or less erect while the leaf-bearing branches assume a diageotropic position. Young branches come up above the older branches, and these are at first ascending naked, but later turn into a horizontal plane at the tip and produce smaller leaf-bearing lateral branches. The leaves do not regenerate either when attached to stem segments or detached. Segments of the older, lower stems produce protonemata from the cut bases. These never arise from the epidermis, but always from the cells of the central region of the stem. If the leafy side branches of the lower stem are cut off, they sprout at the base in the same way as the larger stem segments and nowhere else. If, however, they are left attached to a small seg-

ment of the main stem, they develop long slender rhizoid-like outgrowths from their apices. These are so numerous and are crowded so near the tip as to give an appearance like that of a little brush.

The tips of the ascending, naked branches produce no outgrowth of any sort. Segments cut from near the tips of these branches are likewise devoid of outgrowths, but segments cut from the bases near the main stem produce protonemata from the centers of the bases exactly as the segments of the main stem do.

* *Mnium punctatum* (L.) Schreb. — Stem segments, and both stem leaves and perichaetial leaves, develop protonemata though they are rather tardy about it, requiring forty days for the process. This is so unusual as to suggest that the sample of the species used may not have been in good condition, though its appearance did not indicate this in any way.

* *Mnium punctatum* var. *elatum* (L.) Schreb. — Stem segments and pieces of leaves produced protonemata in eight days. Entire leaves regenerated much more slowly. Perichaetial leaves regenerated as well as stem leaves. Leafy branches arise from the protonemata within a shorter time than in any other species studied.

* *Mnium stellare* Reich. — A number of plants which had been kept in a moist chamber for two weeks had put out many very slender branches bearing reduced leaves. When cut into segments in the Marchal solution these branches regenerated as readily as segments of the older stems. The reduced leaves failed to grow, though normal leaves regenerate readily.

* *Neckera pennata* (L.) Hedw. — The leaves of this species do not regenerate, but stem segments develop protonemata along the sides from the epidermal cells.

* *Rhytidiadelphus triquetris* (L.) Warnst. — The leaves do not regenerate, but protonemata are produced on stem segments. These outgrowths are never produced on the surface of the stems, but from the center of the cut stems, and always at the basal end as in *Hylocomium splendens*.

* *Stereodon lindbergii* (Mitt.) Warnst. — No regeneration was secured from leaves. Stem segments produced protonemata from the bases or near the bases in eleven days.

Results with Benecke's solution

Some trials were made with parts of gametophytes in Benecke's solution alone in capsules, but most of the species were tried out on agar made with Benecke's solution. These petri-dish cultures were kept in a greenhouse built on the north side of the laboratory and in the court of the building. The light received by the cultures was rather weak. In addition to this circumstance most of these tests were made in November and December and regeneration was much slower than in more favorable seasons of the year.

* *Aulocomnium heterostichum* (Hedw.) Br. & Sch. — Stem segments and detached leaves produced protonemata in sixteen days. The behavior, in general, is much like that of *A. palustre* in the Marchal solution.

* *Bartramia pomiformis* L. — Detached leaves regenerated in twenty-seven days.

Catherinea undulata (L.) Web. f. & Mohr. — Leaves detached from stems produced protonemata, but required seventy days. These leaves, however, were planted in November, which is about the least favorable time of the year for growth of plants in general, and has proved unfavorable for growth of both sporophytes and gametophytes of mosses. This was the only species of the Polytrichaceae which could be caused to regenerate in these experiments.

Ceratodon purpureus (L.) Bird. — Stem segments regenerated in thirty days in spite of the unfavorable season. Leafy gametophytes were produced in forty-four days. The leaves, however, did not produce any growth. This is in accord with the results of Heald (3), who kept leaves alive for a long period, but could not induce them to grow. It was expected that the stems would grow, as both Heald and Westerdijk (12) had induced them to grow in culture, while Robbins (8) was able to grow the species in sugar-containing nutrient solutions, even in the dark.

* *Fissidens cristatus* Wills. — Detached leaves produced protonemata in thirty-five days, but branches did not regenerate at all. This is in marked contrast to the behavior of *F. adiantioides* in the Marchal solution. In the latter case the leaves did not

regenerate at all, but the branches developed outgrowths at the tips and along the under side of the stems.

* *Fissidens osmundioides* (Sw.) Hedw. — This species behaved like the preceding one.

* *Mnium affine ciliare* (Grev.) C. M. — This species was tried in the summer and produced protonemata and buds in fifteen days on both stem segments and detached leaves.

Mnium punctatum var. *elatum* (L.) Schreb. — This species was tried on the Marchal solution and the results are given with those of the other species on that solution, but the behavior on Benecke's agar is sufficiently different from that on the Marchal solution to deserve comment. The leaves, whether attached to stem segments or detached, regenerate readily, as do pieces of leaves also. Stem segments produce protonemata in abundance. On Benecke's agar all the leaves first produce aërial rhizoids, which later branch into protonemata with cells which are curiously swollen at one end. The rhizoids which produce protonemata extend horizontally from the leaf for some distance before coming into contact with the agar. The protonemata at the ends of these rhizoids soon bear buds, and later leafy branches. This is quite different from the way the leafy branches arise in the Marchal solution, where they are produced on short protonematal outgrowths very near the leaf.

On many of the leaves on Benecke's agar vertical rhizoids are produced which extend upward for nearly a centimeter and then branch elaborately in the air. These curious rhizoids never developed any protonemata during the time they were observed.

* *Rhodobryum roseum* (Weis.) Limpr. — The detached leaves of this species regenerated protonemata, but took a rather long time, sixty-six days. Here again, however, the unfavorable season may be blamed, since the trial was begun in November.

Trials of other media

A few species, *Mnium affine ciliare, Dicranum flagellare, D. undulatum* and *D. viride,* were tried out on agar made with distilled water without any nutrient salts. These trials gave practically the same results as those with the Marchal solution and with Benecke's agar. This indicates that, in some species at least, the presence of a moist substratum is the most important factor in the early stages of regeneration. The later development of protonemata and of leafy plants was not studied.

Trials with other gametophytic parts

Some tests were made with calyptrae, paraphyses, antheridia and archegonia of *Mnium punctatum* var. *elatum*, but no regeneration took place. Wettstein (13) was able to secure regeneration of all these organs in some species. The trials made in this investigation were not extensive enough to suggest that American species will behave differently from European species. It is probably only a matter of proper conditions of growth.

Failures of regeneration

A few species of moss failed to show any regeneration either on the Marchal solution or on Benecke's agar. Most of these were tried repeatedly, and stem segments, old leaves, young leaves and pieces of leaves were used. Detached leaves and leaves attached to stems failed, and no better success was secured at one season than at another.

As has been noted, *Catherinea undulata* is the only species of the Polytrichaceae which gave regeneration in these tests. *Polytrichum commune*, *P. juniperinum* and *P. piliferum* were tried repeatedly without result. Heald (3) and Westerdijk (12) secured regeneration of *P. commune* in Europe, though the time needed was long, six weeks being required in Heald's studies. The writer kept leaves of the three species named for a much longer time than this, but they finally died without even the beginnings of protonemata.

Climaceum americanum and *C. dendroideum* failed to give regeneration of any sort: this was also true of *Leucobryum glaucum* and *Dicranum montanum*. Limpricht (4) states that the beginnings of protonematal growths can frequently be found on detached leaves of *Leucobryum glaucum*, and that the apex of the end bud has been known to produce a protonematal outgrowth in nature. In these experiments the leaves survived for a long time but did not grow.

The case of *Dicranum montanum* is surprising in view of the ease with which protonemata were secured in all the other species of the genus which were tested.

The growth of gametophytes in moist chambers

In connection with these experiments the gametophytes of a number of species were kept for some time in moist chambers. In several of these the moist atmosphere and reduced light induced a dense growth of rhizoids along the stem. This is the response which these species make to contact with moist earth and is a stage in regeneration. Some species develop these rhizoids in nature in damp situations, but are free from them in drier situations. In *Dicranum scoparium* the stems are normally so clothed, and it would be interesting to see whether an unusually dry atmosphere around the stems would suppress this growth.

The various types of propagula, gemmae, brood bodies, reproductive branches, etc., represent stages in regeneration, and these are induced, or at least encouraged, by a moist atmosphere. This was evident from the growth in moist chambers. Experimental evidence to show that such reproductive bodies are suppressed by a dry atmosphere is lacking, but observations by the author indicate that this is so.

It is noteworthy that none of the species, such as *Polytrichum commune*, which normally live in rather dry places, develop rhizoids or other outgrowths on the stems in the humid atmosphere of the moist chamber. It may be argued that these species are so adapted to life in places where vegetative reproduction by such outgrowths is rarely possible that they have lost, or have never developed, the power to form such growths. These forms are limited to vegetative spread by underground branches or branches in the moist humus at the base of the colony.

In each of the species observed the behavior in moist chambers is consistent with the method of vegetative reproduction in its natural home.

Behavior of submerged gametophytes of land mosses

An attempt was made to secure a cross between *Mnium punctatum* and *Mnium affine* by using the technique of Wettstein. The archegonial heads were cut off, leaving only a short stem below the perichaetial leaves. These stems were fixed in a thin disk of cork which was floated in a jar of Benecke's solution. The antheridial heads were cut off in the same way, but not floated on disks. They sank to the bottom of the jar and the sperms were thus given a chance to swim out into the solution. The disk bearing the archegonial heads was inverted for a time to bring the archegonia into the solution so that the sperms might reach them. The disk was then righted so that the archegonia were lifted out of the solution to allow the sporophytes to grow.

No sporophytes were produced, but the archegonial heads were left in the solution for seven weeks, and the antheridial heads were left at the bottom of the jar immersed in the solution for a similar length of time.

The archegonial heads floated rather low in the water, so that they were partially immersed. No rhizoids or protonemata were produced at any time. The leaves remained perfectly green and appeared to be very healthy. On examination the leaves proved to be very hard and they broke into pieces with the slightest bending.

The antheridial heads at the bottom of the jar did not produce any rhizoids or protonemata, but they sent out very long, slender branches extending up to the surface of the solution. The leaves of these plants were also hard to the touch like those of the other sex.

Presumably the hardness of the leaves was due to a deposit of calcium carbonate upon them. A number of mosses growing in habitats rich in lime show crystals, or even extensive incrustations of this substance, so that these plants must be included among the marl-forming species. It is not so easy to explain the absence of protonemata or rhizoids in species which regenerate easily. The long branches produced by the totally submerged heads are probably an attempt to reach the surface and find better growing conditions. No other species have been tried as yet under such conditions, but this isolated instance of land species living partially or totally submerged suggests that many mosses may endure submergence for rather long periods.

Localization of regenerative power in the organs of mosses

These experiments indicate that there is some tendency for regenerative power to be localized in special reproductive structures, which is in accord with the observations of many workers. This localization is not, however, so fully developed as many think. Species which have special reproductive organs are not incapable of regeneration in other parts, as is shown in *Aulocomnium palustre,* which has well-developed gemmae, but which can reproduce itself by leaves and by stem segments.

It is apparent that the parts most likely to come into contact with the earth are most likely to produce protonemata in culture. Stems, more often than leaves, are capable of regeneration, and stems are more likely to be in contact with the earth at their bases than any other organ. This idea works out well in *Hylocomium splendens,* in which the older stems regenerate readily, though the upper ends of the ascending branches are incapable of regeneration. The lower branches will regenerate at the tips while still attached to stem segments. These stems and branch tips are the parts most likely to come into contact with the earth in nature, but there is much less chance of the young ascending branches making such contact. The fact that species which usually grow in dry places where their stems or leaves rarely touch moist earth do not regenerate in culture has been mentioned. The species of Climaceum are good examples.

The effect of size of organ on regeneration

This subject needs further study. In these experiments it is shown that the leaves of most small-leaved species do not regenerate on the Marchal solution. Sometimes these leaves do regenerate if attached to stem segments, and the large leaves of such forms as *Mnium punctatum* var. *elatum* produce protonemata readily. The small leaves produced on long slender branches of *Mnium stellare* grown in moist chambers do not regenerate, but normal leaves do produce protonemata.

It is possible that regeneration is conditioned by food reserve in these forms. Carlson (1) has shown that cuttings of varieties of Rosa which are low in stored starch do not root, though other varieties with abundant supplies of stored starch grow readily from cuttings. Since rather small pieces of leaves of *Mnium punctatum* var. *elatum* produce protonemata, it is evident that the idea of the necessity of food reserve as a limiting factor cannot safely be emphasized, but a study of the food storage of mosses in connection with regeneration might be profitable.

Regeneration of the gametophytes of liverworts

Stem segments and detached leaves of liverworts were tested for regeneration in the Marchal solution under conditions similar to those obtaining in the moss cultures. The following species were tried, some of them repeatedly: *Bazzania trilobata* (L.) S. F. Gray, *Calypogeia trichomanis* (L.) Corda, *Jamesoniella autumnalis* (DC.) Steph., *Porella platyphylloides* (Schwein.) Lindb., *Ptilidium ciliare* (L.) Nees, *Ptilidium pulcherrimum* (Wed.) Hampe., *Riccardia latifrons* Lindb., *Trichocolea tomentella* (Ehrh.) Dumort.

Not one of these ever showed any sign of regeneration. In most of them the parts faded and died in a short time; in others they survived for some time, but ultimately died without any outgrowths. None of these species were tried on Benecke's agar.

THE REGENERATION OF SPOROPHYTES

The studies on the regeneration of sporophytes by the Marchals (5–7) are widely known, but prior to their investigations the fact that protonemata and gametophytes would develop from setae was noted by Stahl (11) and others. Recently the results of the Marchals have been extended by Wettstein (13), who has studied in detail a number of species and varieties as well as several hybrids between different types. It was the hope of the writer to secure similar data on American species, but the failure to persuade the diploid gametophytes to produce sex organs has prevented a realization of that hope. Diploid gametophytes have been produced, however, from a number of species heretofore unstudied.

Preliminary trials were made with the Marchal solution as a nutrient, but later Benecke's agar proved so much better that it was used in the greater part of the investigation.

In all the experiments the setae of the young sporophytes were cut off at the basal end just above the foot and at the upper end immediately below the apophysis of the capsule. The setae were thoroughly washed with distilled water and laid on plates of Benecke's agar in petri dishes. The cultures were kept in a greenhouse on the north wall of the laboratory, where they received a weak light. The temperature of the greenhouse averaged about 18° C., but sometimes fell during cold nights in winter to 10° C. or even below this.

Some of the cultures remained free from contaminations of any kind, but in others colonies of bacteria and fungi developed. Apparently, these organisms seldom interfered with the development of protonemata. Some cultures were washed with a very weak solution of potassium permanganate, which inhibited the growth of bacteria and especially of molds. In others the setae were washed and transferred to fresh plates of agar.

When the setae were very slow to regenerate, blue-green and green algae sometimes developed in the cultures and were very troublesome. Treatment with a solution of copper sulphate at a concentration of one part per million was sometimes beneficial in inhibiting or killing the algae and seemed not to harm the setae.

Species in which setae were regenerated

The species in which protonemata and leafy plants were secured by the regeneration of setae are listed below. Gametophytes of species marked by an asterisk (*) have never before been produced from setae.

Amblystegium serpens (L.) Br. & Sch.
* Aulocomnium heterostichum (Hedw.) Br. & Sch
Bryum caespiticium L.
* Catherinea undulata (L.) Web. f. & Mohr.
Ceratodon purpureus (L.) Bird.
* Ditrichum pallidum (Schreb.) Hampe.
* Fissidens cristatus Wills.
Funaria hygrometrica (L.) Schreb.
Mnium affine (Grev.) C. M.
Mnium cuspidatum (L.) Leyss.
* Mnium rostratum Schrad.
* Physcomitrium turbinatum (Mx.) Brid.
* Polytrichum commune L.
* Polytrichum ohioense R. & C.

The effect of age of setae on regeneration

The best results were obtained with setae which were nearly full grown while the capsules were yet small. Regeneration usually did not take place from setae which had developed much red color. This red coloration is characteristic of the mature stage in many mosses. Sometimes regeneration was secured at the tip of a seta which had already turned red at the base, but usually the regenerating region was still green in color.

Rate of regeneration of setae

Amblystegium serpens and *Ditrichum pallidum* showed a beginning of protonematal growth in ten days, but at the extreme of slowness *Mnium affine* required eighty-nine days to achieve the same result. The other species of Mnium were also very slow to begin growth. So far as season is concerned, the spring and early summer are best for regeneration, and the late autumn and early winter are least favorable, just as was true of gametophytic regeneration.

Development and appearance of the diploid gametophytes

The diploid gametophytes agreed in their development with those studied by the Marchals and by Wettstein. They were smaller and weaker than the haploid gametophytes grown in nature, but they did not differ from them in any essential character. Their growth was slow and this, as well as their small size, was probably due to the low light intensity in the greenhouse.

None of the diploid gametophytes ever produced sex organs, so it was impossible to secure tetraploid gametophytes as the Marchals and Wettstein had done. Most of the species were kept under observation for more than a year, but failed to reproduce at any season.

Species in which setae failed to regenerate

The following species failed to produce protonemata from the setae of their sporophytes in numerous trials in the Marchal solution and on Benecke's agar:

Dicranum flagellare Hedw.
Dicranum montanum Hedw.
Dicranum scoparium (L.) Hedw.
Dicranum undulatum Ehrh.

Most species of Dicranum show such strong regenerative power in their gametophytes that it is rather surprising that this genus is the only one which failed to give results in these experiments. Wettstein tried *Dicranum scoparium* and *Dicranum undulatum*, but failed to secure regeneration from the sporophytes.

Wettstein also failed with all the members of the Polytrichaceae which he tested. In the present experiments *Catherinea undulata, Polytrichum commune* and *P. ohioense* were regenerated without difficulty, though, as has been noted, no regeneration from gametophytic tissue was secured in any species of Polytrichum.

Ceratodon purpureus would not regenerate for Wettstein, but was easily led to produce protonemata from setae in these trials. Stahl (11) reported that this species produced protonemata from sporophytes, probably the earliest record of such an occurrence. Correns (2) and the Marchals also have succeeded with this species.

EXPERIMENTS ON THE NUTRITION OF THE SPOROPHYTE

A number of gametophytic shoots of *Mnium punctatum* bearing very young sporophytes were cut off 5 millimeters below the perichaetial leaves. Three of the perichaetial leaves were left on each of these stems and the others stripped off. The cut stem ends were now sunk in a layer of Benecke's agar in a petri dish.

The stem ends soon sent out numerous rhizoids into the agar, and each stem developed one or two side branches above the agar. The sporophytes developed normally, though they were rather longer and more slender than usual, perhaps because of the weak light in the petri dish. By accident the agar was allowed to dry out just before the spores were formed, but, since the cultures had grown for more than three months, it appeared that full development of the spores would have taken place.

In another experiment a number of young sporophytes of *Dicranum montanum* were cut off at the base just above the foot. The cut ends were thrust into plates of Benecke's agar in petri dishes. At the beginning of the experiment the capsules were indicated only by green tips on the ends of the setae, but had not become swollen or differentiated. The cultures were kept in a greenhouse with a north light, and the agar was moistened occasionally with Benecke's solution to prevent it from becoming too dry.

The sporophytes continued to grow, but never developed any protonemata at the bases. The capsules grew to maturity and normal size. When ripe, they were found to be more flaccid than normal capsules, but in all those examined the operculum and the peristome were perfectly developed.

The spores appeared to be less numerous than in normal capsules, though this was not certain. So far as one could tell by microscopic examination, these spores were entirely normal, but when planted on Benecke's agar they failed to germinate. In the absence of any data on the viability of spores of *Dicranum montanum* grown in the normal way, it is impossible to say whether the lack of viability was, or was not, due to the conditions of growth of the sporophyte. In any case the growth to maturity of sporophytes while separated from gametophytes indicates a degree of independence of the gametophyte greater than is commonly supposed to exist.

SUMMARY AND CONCLUSIONS

1. Regeneration of protonemata from gametophytic tissue was secured in twenty-four species. In twenty of these species regeneration in culture has not been reported heretofore.
2. Species of Polytrichum and Climaceum failed to regenerate from gametophytic tissue. *Leucobryum glaucum* and *Dicranum montanum* also failed to develop reproductive outgrowths.
3. The presence of a substratum of suitable moisture content seems to be a very important factor in regeneration, though it is suggested that the presence of a reserve food-supply may be of importance.
4. Considerable variation is shown in the rate and in the type of regeneration in the different species.
5. Species which normally produce special reproductive bodies are capable of regeneration from foliage and from stems.

6. The development of diploid gametophytes from the setae of sporophytes was secured in fourteen species. In nine of these species such regeneration has not been secured before this time.

7. It is indicated that the sporophyte may be more nearly independent of the gametophyte than it is commonly supposed to be.

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FRUIT-TREE MYCORRHIZA AROUND ANN ARBOR, MICHIGAN *

ALEXANDER H. SMITH

OUR knowledge of the distribution, in regard to hosts, of the various types of mycorrhiza has become quite extensive. In the past most attention seems to have been given to forest trees and orchids, but the spermatophytes and pteridophytes as a whole have been pretty well examined. Since the extensive studies of Stahl (7), a great deal of work has been done along this line.

Inasmuch as there is very little literature dealing with mycorrhiza on fruit trees (1), it seemed desirable to make a study of a local area with the view of determining to what extent mycorrhizas are to be found on the roots of fruit trees in this country, something of the conditions prevailing when they do occur, and the type which may be present.

The outdoor work was begun October 3, 1928, and continued until the frozen ground about the middle of December made further examination difficult. A long period of weather too dry for fungi of the type which are believed to form mycorrhiza preceded October, but from the middle of October on copious rains supplied plenty of moisture for soil-growing mycelium.

Orchards of very different types were selected for study. Several orchards east of Ann Arbor on Geddes Road were well cultivated and the trees were young and vigorous. In other orchards in this vicinity the trees were well cared for, but the soil had been in grass for a number of years. In several orchards west of Ann Arbor, however, different conditions prevailed. The trees were old and gnarled, and the presence of the fruiting-bodies of *Fomes applanatus*, as well as of numerous rotten knot holes, indicated clearly their unhealthy condition. The fallow ground in such orchards was covered with weeds of all sorts. Other exceptional conditions were found in an old orchard on a steep side-hill which had been overgrown by the common locust; and in a plum thicket which had grown up in humous soil.

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The laboratory work consisted of a histological study from prepared slides in order to examine the details of the root and fungus relation, and to be able to make comparisons with previous studies of mycorrhiza, such as those of Boulet (1), Gallaud (2), Lohman (3), Shibata (6) and others.

This study was made under the direction of Dr. C. H. Kauffman, to whom the writer is greatly indebted for guidance.

ENDOTROPHIC MYCORRHIZA

Endotrophic mycorrhizas were found on all the trees which were examined. The ectotrophic type was not present — not even in situations which favored its development on other species of trees. Tests were made on 30 apple, 14 pear, 12 plum, 6 cherry, and 2 peach trees. The number of mycorrhizas varied considerably in the different habitats, but they were never entirely lacking.

The only certain method of determining which of the rootlets were mycorrhizas, and which were not, was by cutting free-hand sections from them. As a general rule the infected rootlets had the beaded appearance so often connected with endotrophic mycorrhiza. There were, however, many variations from this condition. Often rootlets which appear to be perfectly normal, even to the extent of having numerous root hairs, were found to be infected. Other rootlets which were very crooked and uneven did not possess any fungous mycelium. The color of the normal and the infected rootlets was very similar, but badly infected specimens appeared rather yellow when compared with the whiter normal rootlets. This difference, however, was not consistent.

Since the species of tree apparently had no bearing on the number of mycorrhizas present, and since the difference in habitat did seem to be important in this respect, the discussion will be based on the habitats. These were as follows: orchards with sandy, cultivated, well-drained soil; those with a clayey soil, cultivated, but poorly drained; those on well-drained sod land; single trees growing on humous soil; and, lastly, an old orchard on a steep side-hill which was overgrown with locust.

In regard to position, their depth varied somewhat depending on the habitat, but they were always found relatively close to the surface. They were always present in cultivated soils. Here the roots near the surface had been destroyed by plowing, and shoots from the roots lying deeper were penetrating into the cultivated area. These branches were often heavily infected, and had a rosette appearance which caused them to resemble the witches'-brooms of forest trees. Consequently, in such places, most of the mycorrhizas were found at a depth of six or eight inches. In sandy areas some were found as deep as ten inches. This, however, was quite exceptional. In places near the trees, where plowing had not destroyed the roots, mycorrhizas were found on the rootlets nearest the surface as well as at the depths mentioned previously. The same general distribution in regard to depth which has been cited above was also true for mycorrhizas in sod land, with the possible exception that they did not occur at as great a depth. Eight inches was the maximum. In fallow ground they were distributed fairly evenly throughout the upper six or eight inches of the soil. In the peculiar side-hill situation mentioned, mycorrhizas were found to occur within the upper three inches of the soil. Here, owing to the shade of the apple and locust trees, no undergrowth was present. Running water from rains had caused some erosion, and the layer of loam or surface soil remaining was not more than an inch or two deep anywhere, and it was often lacking. In the humous habitats studied, mycorrhizas were always present in the humus, but few were found in the soil beneath.

Mycorrhizas were equally numerous on all parts of the root-system which were near the surface, i.e., the rootlets at the very base of the tree were as likely to be infected as those farther out.

The manner of occurrence is that which is commonly reported for the type on forest trees. They are usually found in clumps or masses. Single infections are rare, and no doubt indicate an early stage of development. It seems that the formation of mycorrhiza stimulates the formation of lateral roots which in turn become infected and thus the large clumps develop.

The number of mycorrhizas in the different habitats varied greatly. In the cultivated sandy loam, humus and sod land they were very abundant. In the cultivated clayey soil and in the peculiar side-hill situation, the number was noticeably small.

There are several factors which may control the abundance of mycorrhiza. The temperature, moisture and type of soil are no doubt the ones which affect fungi most. Local variations in these, then, should to some extent account for the different numbers of mycorrhiza. In this work the type of soil, the moisture and drainage were the most widely differing factors. Thus one may expect to find in them some explanation for the variation in numbers. Since large numbers were found in various types of soil, this factor may seem to be of secondary importance. As is well known, however, organic material must be present in the soil to sustain fungous life, and a lack of such material would preclude the presence of fungi. Obviously, then, the relative amounts of food material in the soil — for mycorrhiza-formers are soil-dwelling fungi — would have a direct bearing on the amount of mycelium present. The more mycelium there is present the greater are the chances of the rootlets to become infected.

The moisture content of the soil is as important to fungi as to any other plant. As is well known, in dry years one finds very few fungous fruiting-bodies as compared with the number found in years of copious rainfall. Since good vegetative development must precede abundant fruiting, the relation of moisture to mycelial growth is apparent.

Of all the habitats studied, the two which contained the smallest numbers of mycorrhizas were characterized by extreme moisture conditions. The clay was very wet, while the hillside was very dry. In addition to this, both situations contained relatively small amounts of organic material. Since both the factors vary greatly from the normal conditions existing in orchards, and since both tend to produce unfavorable living conditions for the fungus, they no doubt account for the scarcity mentioned.

The pH values of the various soils were not taken. Previous work (3) has shown that mycorrhizas occur in soils ranging from pH 4.9 to 8.2.

The material used in the histological studies was killed and fixed in weak chromo-acetic fixing solution. The sections were cut from paraffin and stained in Delafield's haematoxylin with safranin as a counter stain.

The sections showed the usual facts concerning the details of the fungous mycelium and its relation to the root (see Plate XXXIII). In the rootlets of apple, pear and plum the arbuscles and vesicles described first by Gallaud (2) for endotrophic mycorrhiza in general, and later by Boulet (1) for the mycorrhiza of fruit trees, were present here also. The entrance of the fungous hyphae into the epidermis was also observed. A hypha lying against the root may give off branches which penetrate the epidermal cells directly. The area in which infections occur lies in the region of the root hairs as well as a short distance farther back. After developing in the epidermal cell, the hypha penetrates into the cortical cells where it develops freely. For the most part it develops longitudinally and tangentially, and is seldom found next to the stele. In old infections the hyphae are not numerous in the epidermal cells. The connection between the interior hyphae and the mycelium lying outside the root seems to be of short duration. It was never found in old specimens.

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DESCRIPTION OF PLATE XXXIII

The following figures show the fungous hyphae, as well as such structures as vesicles and arbuscles, in the rootlets of the various species of tree studied. The following abbreviations are used: *s*, sporangiole; *v*, vesicle; *a*, arbuscle; *n*, the cell nucleus. All the figures were drawn at a magnification of approximately 500 and reduced to 350

FIG. 1. A longitudinal section through the cortex of an apple rootlet showing the hyphae in the cells

FIG. 2. A longitudinal section through the cortex of a cherry rootlet showing the hyphae in the cells

FIG. 3. A longitudinal section through the cortex of a plum rootlet

FIG. 4. A longitudinal section through the cortex of a pear rootlet showing a single hypha passing through several cells

FIG. 5. A vesicle in an apple rootlet

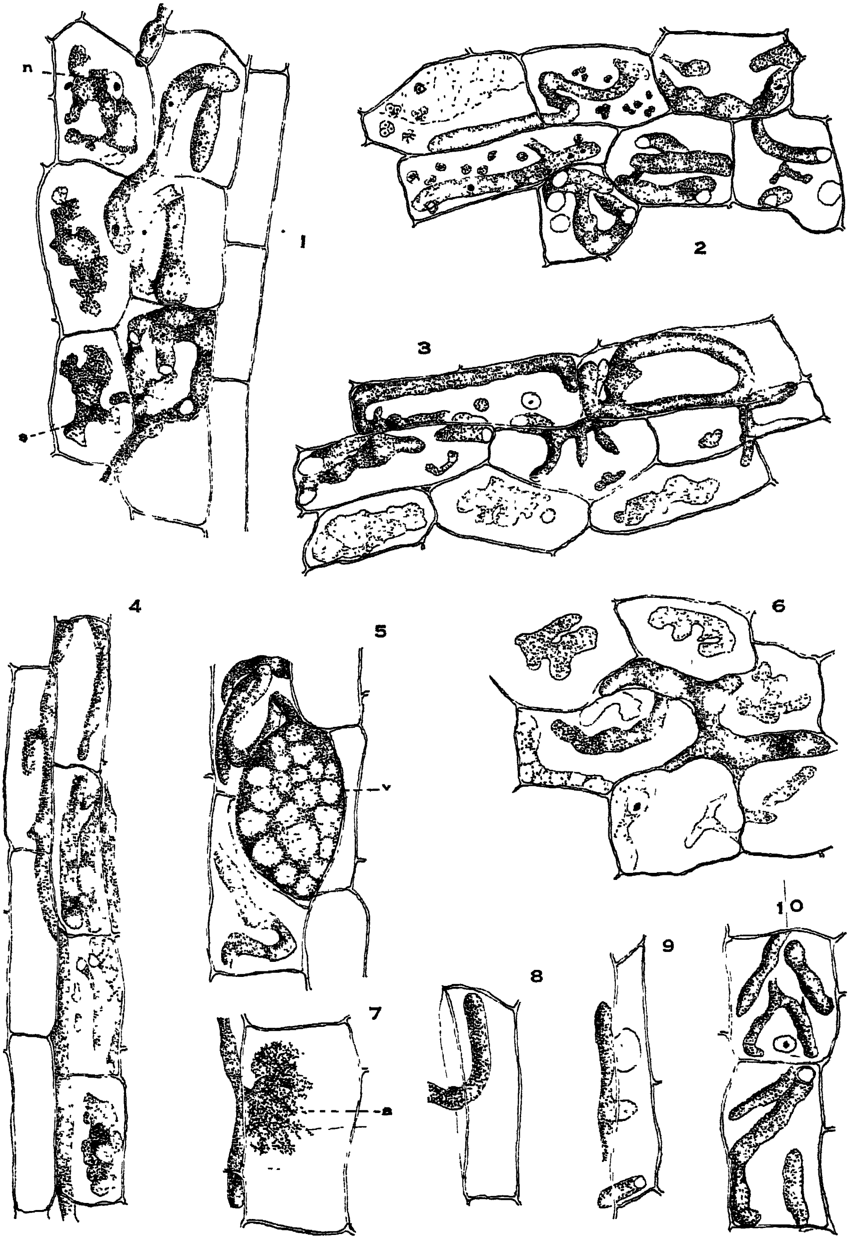
FIG. 6. A longitudinal section showing an intercellular hypha in an apple rootlet

FIG. 7. A single cell from the cortex of an apple rootlet showing an arbuscle

FIGS. 8–9. Epidermal cells of an apple rootlet showing the entrance of hyphae

FIG. 10. Cells from the cortex of a peach rootlet with hyphae

PLATE XXXIII



FACTORS RESTRICTING THE DISTRIBUTION OF COLOR PIGMENTS

Factors D, T and F are all members of the linked group to which B and P belong. All five of these factors have certain characteristics in common. They all influence the color of the anthocyanin pigment formed, D, T and F being identical in this respect, and all of them have the power of overcoming the partial inhibiting effect on the production of anthocyanin of factor U in the combination RNU. Anthocyanin formed under the influence of P is purple throughout the cell, that formed under the influence of B is blue at the inner and rose purple at the outer end of the cell, while that formed under the influence of D, T or F is deep blue throughout the cell. R and N must, of course, be present before anthocyanin is formed.

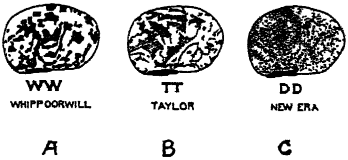


FIG. 5. Various types of pigment distribution brought about by factors indicated in the figure. Whippoorwill, Taylor and New Era are names of well-known cowpea varieties with the markings shown

The characteristic peculiar to factor D is the restriction of anthocyanin in the seed coat to certain groups of cells thickly scattered over the seed coat. Outside these groups the surface color is due to whatever melanin-like pigment may be present (usually buff or red). Perhaps the action of D might be more accurately described by saying that it prevents the formation of anthocyanin pigment in the palisade cells except in certain groups of cells thickly scattered over the seed coat, and at the same time causes all the anthocyanin pigment that does form to be deep blue in color.

PIGMENT DISTRIBUTION IN COWPEA VARIETIES

New Era. — Figure 5C shows the appearance of seeds homozygous for D. It was drawn from a seed of the New Era variety. The blue dots are irregular in outline and just large enough to be easily visible to the unaided eye. They are thickly and quite uniformly scattered over the entire surface of the seed. Since D is allelomorphic to B and P, these blue dots cannot occur in individuals homozygous for *B* or *P* (see Table V, Crosses 229, 231). But in individuals heterozygous for *D* and *P* the dots are easily observed. In those heterozygous for *D* and *B*, part of the seed coat is usually shining black, other parts being similar to the surface of New Era peas. The black surface in such cases varies all the way from nothing to practically the entire seed coat, even in the seeds of a single plant.

Since the factor *N* is absent in maroon and coffee seed coats, no anthocyanin pigment is formed. Both these colors involve factor *B* and hence cannot be homozygous for *D*. When heterozygous for both *D* and *B*, the seed coat has patches of maroon or coffee pigment according as *U* is absent or present, interspersed with patches that indicate clearly the presence of *D*, although no anthocyanin pigment is formed. The pigment in the dots in these cases appears to be slightly darker than that outside the dots, but no examination was made to determine what difference there may be in the pigments within and without the dots.

If we remove the factor *N* from the New Era type of cowpea, the dots due to *D* are still visible, but the pigment in them is not blue. The appearance of the entire seed coat becomes identical with that of the dotted areas described in the last paragraph.

If *D*, *N* and *R* occur without *U*, the resulting seed coat is red, with the blue dots due to *D*. Outside the blue dots the seed coat is pigmented as in red varieties. If we drop *N* out of this combination we get pink seed coat. In this case the blue dots disappear, and their place becomes indistinguishable from the remainder of the seed coat.

Taylor. — Factor *T* is in all respects identical with *D* except that the dots are more thinly scattered over the surface of the seed and occur more or less in well-defined groups, leaving considerable areas without dots (see Figure 5B). In crosses between *D* and *T*, *D* is epistatic to *T*, and the F_2 generation consists of three *D*'s to one *T*. There is little difficulty in distinguishing these two types (see Table V, Crosses 215, 229, 240, 251, 424).

Blue. — Factor *F* is similar in its action, in most respects at least, to *D* and *T*, except that it causes concentration of the blue pigment in scattered individual cells here and there over the surface of the seed coat (see Table V, Cross 251). The pigmented cells of the blue are not collected in groups as in the case of *D* and *T*, though they are very numerous. The result is a beautiful blue seed coat, appearing to the unaided eye to be continuous blue, an effect which in reality is due to numerous separated blue points. Another point in which *F* differs from *D* and *T* is in the matter of dominance. *D* and *T* are fully dominant factors, while the dominance of *F* is highly variable. Many individuals heterozygous for *F* show no sign of its presence, while others of identical parentage and genetic constitution show much blue coloration. There is even much variation in the degree of the blue coloration of individuals homozygous for *F*, the cause of which is unknown. In general, the blue color due to *F* cannot be satisfactorily made out except on a buff background.

The factor *F* was originally found in a blue variety of cowpea from Brazil. About half the seeds of this variety were plain blue, the other half being blue Taylor; that is, they had both the blue coat due to *F* and the blue dots due to *T*. This proved to be a case of complete linkage between factors *T* and *F*, and in no case have the writers been able to break up this combination. The plain blues, with the exception of one individual mentioned in the next paragraph, all contained the *T* factor along with another factor, *X*, which prevented the *T* factor from coming to expression.

Taylor inhibitor. — In one individual amongst the plain blues of the Taylor variety, the writers found the factor *F* present without *T*. No Taylor dots appeared in any of its progeny. It was crossed with one of the varieties commonly grown in this country. But every other plain blue used in any of the writers' numerous crosses gave progeny which in every case showed the Taylor dots, even in the F_1 generation. This suggested the presence in these plain blues of a recessive inhibiting factor for Taylor dots, a suggestion which proved to be fully justified by the counts in numerous families. To this inhibiting factor the symbol *X* was given. It had no effect on factor *F*. Whether it would suppress the dots due to factor *D* was not tested.

Wild. — Amongst the original stock of seeds obtained from Professor Piper were some of a wild species from Africa, supposedly the progenitor of our cultivated forms of cowpea. Its visible characters indicated the presence of factors *R*, *N*, *T*, *U* and *W*. These seeds also have patches of black pigment, the area of which is highly variable. Occasional seeds are almost solid black, while others show very little black. This variation occurs on the seeds of the same homozygous plant.

Of several efforts to cross this wild cowpea with cultivated sorts only one was successful, but in this cross the progeny was entirely fertile and large numbers of F_2 and later generation individual were obtained. The segregation of characters that occurred in these generations indicated clearly that the black spotting is due to the influence of a Mendelizing factor, to which the writers gave the name "spotting," with symbol *S*. In its absence the *T* factor gave typical Taylor markings. Black spots similar to these have occurred in all the writers' crosses involving *D* or *T* and *B*, but except when *S* is present these spots occur only in heterozygous individuals.

Whippoorwill. — The well and favorably known Whippoorwill variety of cowpea is characterized by a mottled seed coat like that shown in Figure 5 A. The darker areas resemble coffee seed coat, but the lighter areas are buff or clay-colored. The writers' studies, in connection with those of Mann, have shown that this peculiar mottling is due to the action of a factor that affects the distribution of the melanin-like pigment in the palisade cells, and perhaps also that in the deeper layers. In the darker areas the palisade cells are abundantly supplied with melanin-like pigment; in the lighter areas the amount of this pigment is less.

When *W* is present the Whippoorwill markings are observable in any seed coat, except black, in which there is an abundance of melanin-like pigment (see Table V, Cross 242). Buff varieties display them to best advantage, but these markings are observable in reds, pinks, maroons, coffees and purples, though in the varieties last named the amount of melanin-like pigment may be so small as to render the Whippoorwill markings very indistinct. They are not observable in black seed coats, because of the superabundance of anthocyanin pigment, the distribution of which is not affected by *W*, and possibly also because of the paucity of melanin-like pigment in the palisade cells.

EYE FACTORS

Many varieties of cowpeas have the pigment in the seed coat confined to a small area round the hilum (Figure 6*e*). In others there is a large area of pigment around the hilum, with isolated spots elsewhere on the seed coat (Figure 6*b* and *b*′). In one type the area about the hilum is heavily pigmented, and the remainder of the seed coat less so (Figure 6*a*). In all these types the pigmented area about the hilum is called an "eye." A common table variety is called the Blackeye (Figure 6*e*).

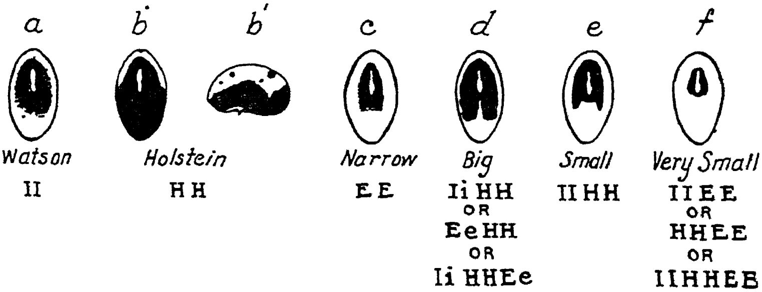


FIG. 6. Types of "eyes" found in cowpeas, with genetic constitution of each

The writers' investigations have shown the existence of three independent eye factors which, either singly or in combination, give rise to five distinct types of eye. These are all shown in Figure 6. In addition there is another fairly well defined type that occurs in certain heterozygous combinations (Figure 6*d*). In a former paper by the senior writer,[3] an account is given of two of the three eye factors, the other factor not having then been recognized.

Mann has shown that the palisade cells in the non-pigmented areas in varieties having eyes are peculiarly misshapen, while the pigmented cells are normal in shape. All three of these eye factors are recessive when crossed with self-colors, but there is partial dominance in certain cases involving combinations of the eye factors (see "Big eye").

[3] Spillman, W. J., "Inheritance of the 'eye' in Vigna," *Am. Nat.*, 45: 513–523. 1911.

The only eye type commonly found in cultivated varieties of cowpeas is that shown in Figure 6*e*. It results when factors *I* and *H* are both present in homozygous condition.

DESCRIPTION

Factor I. —A double dose of factor *I* gives the Watson type of eye (Figure 6*a*), a name under which a variety having this type of eye was received from the Arkansas Agricultural Experiment Station. The region about the hilum is densely pigmented. A short distance from the hilum there begin to appear cells devoid of pigment, or nearly so. These increase in number as the distance from the hilum increases, but in nearly all cases some pigment is found in scattered cells over the entire seed coat. This gives the seed a dirty aspect except when the color of the pigment is itself attractive. Watson eyes of red or coffee pigment present a very pleasing appearance. The total amount of pigmentation in the Watson type of eye varies greatly, for reasons not determined. There is a possibility that this is governed by other factors, but so far this has not been proved.

A striking characteristic of all Watson eyes is the fact that the margin of the densely pigmented area about the hilum is quite indefinite, owing to gradual increase in the number of non-pigmented cells as distance from the hilum increases. It was the indefiniteness of this margin that suggested the symbol *I* for this factor (see Table V, Crosses 201, 206, 307).

Factor H. — The eye type for which factor *H* is responsible is called Holstein, and is shown in Figure 6*b* and *b*′. The pigmented area about the hilum varies in magnitude in different families, from slightly larger than that shown in Figure 6*d* to practically self-color. The extreme tip of the chalazal end of the seed is the last to become pigmented. Besides the large pigmented area about the hilum, pigmented spots, usually rather large and always with definite margins, occur over the remaining surface of the seed. In different families the proportion of pigmented surface varies from about two fifths to nine tenths or more of the entire surface of the seed.

While the Holstein eye seems to be due to a single factor, at least in our material, it appears to be greatly influenced in expression by the presence of other factors (see Table V, Crosses 201, 206). Small and large Holstein eyes may be fixed by selection, but when either small or large eyes are used in crosses there is usually found in the second and later generations the whole range of Holstein eye sizes. Further study of this point would undoubtedly lead to results of no small theoretical interest.

Factor E. — In a variety of cowpeas obtained from Africa there occurred three types of eye, shown in Figure 6 *c*, *e* and *f*. Most of the seeds had eyes of type *e*, and it was not at first noticed that the other two types were present. Certain of these peas used as parents in crosses led to the production in F_2 of eyes of type *f*, Figure 6. This led to a careful reëxamination of the original material, resulting in the finding of a number of seeds having eyes of types *c* and *f*. The final results showed conclusively that type *c* is due to a single factor to which the writers gave the name Narrow Eye, with symbol *E* (see Table V, Crosses 307, 316). This factor *E* was later found concealed in one of the white varieties of unknown origin used in the writers' crosses.

COMBINATIONS OF EYE FACTORS

Big eye. — The type of eye shown in Figure 6 *d* occurs in cowpeas in which factor *H* is homozygous and either or both factors *I* and *E* are heterozygous (see Table V, Crosses 201, 206). In such cases factors *I* and *E* are partially dominant.

In families in which both types *b* and *d* of Figure 6 (Holstein and Big eye) occur there is often difficulty in separating them, especially if the pigmented area of the Holstein types is small. It should be remarked that Big eye practically always has some pigmented spots in addition to the area about the hilum.

Small eye. — To distinguish it from other eye types, the common type of eye shown in Figure 6 *e*, was designated Small eye. It is due to the combination *IIHH* (see Table V, Crosses 201, 206).

Very small eye. — The writers call the type of eye shown in Figure 6 *f*, "very small eye." It results from any of the combinations *IIEE*, *HHEE*, *IIHHEE* (see Table V, Crosses 307, 316).

Note that all these combinations contain *EE*. This type of eye varies somewhat in size, but it is impracticable to separate the various subtypes, owing to the different combinations of factors that form this type of eye.

Genetic constitution of eye types

All the types of eye discussed above may occur in peas with any seed-coat color thus far found, though the colors cannot be satisfactorily classified when the pigment occurs in small areas only.

It is an interesting speculation that these three eye factors may represent somewhat similar mutations in three different chromosomes. The writers might go still further and suggest that these chromosomes are genetically related through a common ancestral form and that the mutation in question occurred in this ancestral chromosome; present differences in expression are due to subsequent evolutionary changes in the chromosome decendants.

Table IV gives the genetic constitution of the various eye types.

TABLE IV

TYPES OF EYE IN COWPEAS WITH THE GENETIC CONSTITUTION OF EACH TYPE

Eye types	Illustration	Genetic constitution
Watson.....	Figure 6a	IIhhee
Holstein....	do. b, b′	iiHHee
Narrow.....	do. 6c	iihhEE
Big........	do. 6d	IiHHee, iiHHEe, or IiHHEe
Small......	do. 6e	IIHHee
Very small..	do. 6f	IIhhEE, iiHHEE, or IIHHEE

OTHER FACTORS

Factor G Dotting. — In certain Holsteins it was observed that the irregular spots of color in that portion of the surface not reached by the area about the hilum were unusually small and very numerous. Subsequent studies showed that this peculiarity is due to a segregating factor for which the symbol *G* was adopted. In individuals heterozygous for this factor the dotting is generally less evident than in homozygous individuals, and there is much variation in this respect. Definite correlation appears to exist between this dotting and certain habits of growth in the vine. The internodes are short and the leaves are thick, rough and crinkled, and are a deeper green than in ordinary forms. The dotting of the seeds occurs only in the Holstein type, or possibly types involving *HH* with other eye factors.

Factor L. — The factor *L* has no direct relation to pigmentation, but is responsible for certain depressions in the surface of the seed. These are irregular in outline, but extend lengthwise in the seed. They are most prominent in the region about two thirds of the way from the hilum to the opposite side. They are caused by slight, irregular ridges that form on the inner surface of the seed pod. This character is mostly recessive, though heterozygous individuals sometimes show a trace of the character (see Table V, Cross 260).

Factor A. — The seed pod of most varieties of cowpeas is straight or slightly sickle-shaped. In a variety obtained from China the pods were curled after the manner of alfalfa seed pods, whence the symbol *A* adopted for the factor controlling this character. Individuals heterozygous for this factor were usually more or less intermediate between ordinary forms and those with curled pods and produced curled, semicurled and straight pods in the ratio of 1–2–1.

EXPERIMENTAL DATA

The breeding results of over 10,000 plants have been used in arriving at the conclusions herein reported. Because of a limitation in space of this publication, however, it has been possible to include only a sufficient amount of the data to indicate the behavior of the various factors. The major portion of the data, which include the results of more promiscuous crossings and support the conclusions arrived at by the writers, has been deposited in the libraries of the University of Michigan, Ann Arbor, Michigan, and

TABLE V

EXPERIMENTAL RESULTS FROM THE HYBRIDIZATION OF VARIOUS COWPEA PHENOTYPES, WITH THE GENETIC CONSTITUTION OF THE INDIVIDUALS INVOLVED

Cross 201 { Parents — Black 13 × Purple Small eye
Genotype — NNBBUURRiihh NNPPUURRIIHH
F_1 = Purple NNPBUURRIiHh

Generation	Nature of previous generation			Purple					Black				
	Phenotype	Genotype		Self	Watson	Holstein	Big eye	Small eye	Self	Watson	Holstein	Big eye	Small eye
F_2 and F_3 from	Purple	NNPBUURRIiHh	Actual	44	12	3	8	2	19	1	2	....	1
			Expected	38.9	13	4.3	8.6	4.3	13	4.3	1.4	2.9	1.4
F_3 from	Purple	NNPPUURRIiHh	Actual	76	25	5	10	6	....	....	...	....	...
			Expected	68.6	22.9	7.6	15.2	7.6	....	....	...	....	...
Do........	Purple	NNPBUURRiiHh	Actual	30	....	6	....	...	7	....	4	....	...
			Expected	26.5	....	3	....	...	3	....	1	....	...
Do........	Purple	NNPPUURRiiHh	Actual	19	....	7	....	...	....	....	...	....	...
			Expected	19.5	....	6.5	....	...	....	....	...	....	...
Do........	Purple	NNPPUURRiihh	Actual	45	....	....	....	...	....	....	...	....	...
			Expected	45	....	....	....	...	....	....	...	....	...
Do........	Purple Watson	NNPPUURRIIhh	Actual	....	26	....	....	...	....	....	...	....	...
			Expected	....	26	....	....	...	....	....	...	....	...
Do........	Purple Watson	NNPBUURRIIHh	Actual	....	16	....	....	4	....	5	...	....	...
			Expected	....	14.1	....	....	4.7	....	4.7	...	....	1.6
Do........	Purple Holstein	NNPPUURRiiHH	Actual	....	....	22	....	...	....	....	...	....	...
			Expected	....	....	22	....	...	....	....	...	....	...
Do........	Black	NNBBUURRiihh	Actual	....	....	....	....	...	61	....	...	....	...
			Expected	....	....	....	....	...	61	....	...	....	...
Do........	Black	NNBBUURRIiHh	Actual	....	....	....	....	...	52	13	4	10	6
			Expected	....	....	....	....	...	47.8	16	5.3	10.6	5.3
Do........	Black	NNBBUURRIihh	Actual	....	....	....	....	...	38	17	...	....	...
			Expected	....	....	....	....	...	41.2	13.7	...	....	...

TABLE V (*Continued*)

EXPERIMENTAL RESULTS FROM THE HYBRIDIZATION OF VARIOUS COWPEA PHENOTYPES, WITH THE GENETIC CONSTITUTION OF THE INDIVIDUALS INVOLVED

Cross 206 {Parents — Black eye 13 × Black 22
Genotype — NNBBUURRIIHH NNBBUURRiihh

F_1 = Black NNBBUURRIiHh

Generation	Nature of previous generation			Black				
	Phenotype	Genotype		Self	Watson	Holstein	Big eye	Small eye
F_2 from.....	Black	NNBBUURRIiHh	Actual	19	5	2	5	....
			Expected	17.5	5.8	1.9	3.9	1.9
F_3 from.....	Watson	NNBBUURRIIhh	Actual	61	...	....	....	....
			Expected	61	...	....	....	....
Do........	Watson	NNBBUURRIIHh	Actual	13	...	....	....	5
			Expected	13.5	...	....	....	4.5
Do........	Holstein	NNBBUURRiiHH	Actual	....	...	35	....	....
			Expected	....	...	35	....	....
Do.......	Big eye	NNBBUURRIiHH	Actual	....	...	19	49	14
			Expected	....	...	20.5	41	20.5

TABLE V (*Continued*)

EXPERIMENTAL RESULTS FROM THE HYBRIDIZATION OF VARIOUS COWPEA PHENOTYPES, WITH THE GENETIC CONSTITUTION OF THE INDIVIDUALS INVOLVED

Cross 215 { Parents — Blue Taylor × Coffee
Genotype — $NN\overgroup{BTF}\overgroup{BTF}UURR$ $nn\overgroup{Btf}\overgroup{Btf}UURR$

F_1 = Black $Nn\overgroup{BTF}\overgroup{Btf}UURR$

Generation	Nature of previous generation			Black		Coffee	
	Phenotype	Genotype		Self	Taylor	Self	Taylor
F_2 and F_3 from	Black	$Nn\overgroup{BTF}\overgroup{Btf}UURR$	Actual	50	13	13	4
			Expected	45	15	15	4.5
F_3 from.....	Black	$Nn\overgroup{Btf}\overgroup{Btf}UURR$	Actual	11	....	3	....
			Expected	10.5	....	3.5	....
Do........	Black	$NN\overgroup{BTF}\overgroup{Btf}UURR$	Actual	8	5	....	....
			Expected	9.7	3.2	....	....
Do........	Black	$NN\overgroup{Btf}\overgroup{Btf}UURR$	Actual	17	....	....	....
			Expected	17	....	....	....
Do........	Blue Taylor	$Nn\overgroup{BTF}\overgroup{BTF}UURR$	Actual	....	11	....	7
			Expected	....	13.5	....	4.5
Do........	Blue Taylor	$NN\overgroup{BTF}\overgroup{BTF}UURR$	Actual	....	6	....	....
			Expected	....	6	....	....
Do........	Coffee	$nn\overgroup{BTF}\overgroup{Btf}UURR$	Actual	....	....	28	7
			Expected	....	....	26.2	8.7
Do........	Coffee Taylor	$nn\overgroup{BTF}\overgroup{BTF}UURR$	Actual	....	....	....	25
			Expected	....	....	....	25

TABLE V (*Continued*)

Experimental Results from the Hybridization of Various Cowpea Phenotypes, with the Genetic Constitution of the Individuals Involved

Cross 223 { Parents — Coffee 27 × Red 4
Genotype — nnBBUURR NNbbuuRR

F_1 = Black NnBbUuRR

Generation	Nature of previous generation			Black	Coffee	Maroon	Clay	Red	Pink
	Phenotype	Genotype							
F_2 from.....	Black	NnBbUuRR	Actual	18	5	2	5	1	....
			Expected	17.4	4.4	1.4	5.8	1.4	.5
F_3 from.....	Black	NnBbUURR	Actual	7	3	....	4	...	....
			Expected	7.9	2.6	....	3.5	...	....
F_3 and F_4 from	Coffee	nnBBUURR	Actual	....	89	....	....	...	....
			Expected	....	89	....	....	...	....
F_3 and F_4 from	Coffee	nnBbUuRR	Actual	....	24	10	7	...	2
			Expected	....	24.1	8.1	8.1	...	2.7
F_4 from.....	Maroon	nnBBuuRR	Actual	....	....	31	....	...	....
			Expected	....	....	31	....	...	....
Do........	Maroon	nnBbuuRR	Actual	....	....	29	....	...	6
			Expected	....	....	26.3	....	...	8.8
Do........	Clay	NNbbUURR	Actual	....	....	....	43	...	....
			Expected	....	....	....	43	...	....
Do........	Clay	NNbbUuRR	Actual	....	....	....	6	7	....
			Expected	....	....	....	9.7	3.2	....
Do........	Clay	nnbbUuRR	Actual	....	....	....	16	...	10
			Expected	....	....	....	19.5	...	6.5

TABLE V (*Continued*)

EXPERIMENTAL RESULTS FROM THE HYBRIDIZATION OF VARIOUS COWPEA PHENOTYPES, WITH THE GENETIC CONSTITUTION OF THE INDIVIDUALS INVOLVED

Cross 229 Parents — New Era 9 × Taylor 14
Genotype — $NN\overset{\frown}{BDt}\overset{\frown}{BDt}UURR$ $NN\overset{\frown}{BdT}\overset{\frown}{BdT}UURR$
F_1 = New Era $NN\overset{\frown}{BD}t\overset{\frown}{BdT}UURR$

Generation	Nature of previous generation			New Era	Taylor
	Phenotype	Genotype			
F_2 from......	New Era	$NN\overset{\frown}{BDt}\overset{\frown}{BdT}UURR$	Actual Expected	24 24	8 8

Cross 231 Parents — New Era × Coffee 27
Genotype — $NN\overset{\frown}{BD}\overset{\frown}{BD}UURR$ $nn\overset{\frown}{Bd}\overset{\frown}{Bd}UURR$
F_1 = Black $Nn\overset{\frown}{BD}\overset{\frown}{Bd}UURR$

Generation	Nature of previous generation			Black		Coffee	
	Phenotype	Genotype		Self	New Era	Self	New Era
F_2 from......	Black	$Nn\overset{\frown}{BD}\overset{\frown}{Bd}UURR$	Actual	9	3	5	....
			Expected	9.6	3.2	3.2	1.1
F_3 from......	Coffee	$nn\overset{\frown}{BD}\overset{\frown}{Bd}UURR$	Actual	...	...	40	13
			Expected	...	...	39.7	13.2

TABLE V (*Continued*)

EXPERIMENTAL RESULTS FROM THE HYBRIDIZATION OF VARIOUS COWPEA PHENOTYPES, WITH THE GENETIC CONSTITUTION OF THE INDIVIDUALS INVOLVED

Cross 240 { Parents — Taylor 14 × Clay 17
Genotype — $NN\widehat{BT}\widehat{BT}UURR$ $NN\widehat{bt}\widehat{bt}UURR$

F_1 = Taylor $Nn\widehat{BT}\widehat{bt}UURR$

Generation	Nature of previous generation			Taylor	Clay
	Phenotype	Genotype			
F_2 from........	Taylor	$NN\widehat{BT}\widehat{bt}UURR$	Actual	20	5
			Expected	18.7	6.2
F_3 from........	Clay	$NN\widehat{bt}\widehat{bt}UURR$	Actual	....	63
			Expected	....	63

Cross 242 { Parents — Whippoorwill 6 × Clay 17
Genotype — $NNbbUURRWW$ $NNbbUURRww$

F_1 = Whippoorwill $NNbbUURRWw$

Generation	Nature of previous generation			Whippoorwill	Clay
	Phenotype	Genotype			
F_2 from.......	Whippoorwill	$NNbbUURRWw$	Actual	37	17
			Expected	40.5	13.5

TABLE V (*Continued*)

EXPERIMENTAL RESULTS FROM THE HYBRIDIZATION OF VARIOUS COWPEA PHENOTYPES, WITH THE GENETIC CONSTITUTION OF THE INDIVIDUALS INVOLVED

Cross 251 { Parents — Blue 20 × Clay 17 F_1 = Blue Taylor
Genotype — $NN\overparen{BTF}\overparen{BTF}UURRXX$ $NN\overparen{btf}\overparen{btf}UURRxx$ $NN\overparen{BTF}\overparen{btf}UURRXx$

Generation	Nature of previous generation			Blue Taylor	Blue	Clay
	Phenotype	Genotype				
F_2 and F_3 from	Blue Taylor	$NN\overparen{BTF}\overparen{btf}UURRXx$	Actual	30	9	7
			Expected	25	8.7	11.5
F_3 from......	Blue Taylor	$NN\overparen{BTF}\overparen{BTF}UURRXx$	Actual	25	9	....
			Expected	25.5	8.5	....
Do.........	Blue Taylor	$NN\overparen{BTF}\overparen{BTF}UURRxx$	Actual	11	....	....
			Expected	11	....	....
F_3 and F_5 from	Blue	$NN\overparen{BTF}\overparen{BTF}UURRXX$	Actual	....	64	....
			Expected	....	64	....

Cross 260 { Parents — Red 2 × Red with longitudinal furrows F_1 = Red with longitudinal furrows
Genotype — NNbbuuRRll   NNbbuuRRLL   NNbbuuRRLl

Generation	Nature of previous generation			Red	Red longitudinally furrowed
	Phenotype	Genotype			
F_2 from........	Red	NNbbuuRRLl	Actual	18	7
			Expected	18.7	6.2

TABLE V (*Continued*)

Experimental Results from the Hybridization of Various Cowpea Phenotypes, with the Genetic Constitution of the Individuals Involved

Cross 307 { Parents — Black Narrow eye 43 × Watson 28
Genotype — NNBBUURRiiEE NNBBUURRIIee

F_1 = Black NNBBUURRIiEe

Generation	Nature of previous generation			Black			
	Phenotype	Genotype		Self	Watson	Narrow eye	Very small eye
F_2 and F_3 from	Black	NNBBUURRIiEe	Actual	69	25	24	10
			Expected	72	24	24	8
F_3 from......	Black	NNBBUURRiiee	Actual	17	....	....	....
			Expected	17	....	....	....
Do.........	Black	NNBBUURRIiee	Actual	13	6	....	....
			Expected	14.2	4.7	....	....
Do.........	Black	NNBBUURRiiEe	Actual	14	....	2	....
			Expected	10	....	7	....
Do.........	Watson	NNBBUURRIIee	Actual	....	18	....	....
			Expected	....	18	....	....
Do.........	Watson	NNBBUURRIIEe	Actual	....	12	....	2
			Expected	....	10.5	....	3.5
Do.........	Narrow eye	NNBBUURRIiEE	Actual	....	....	14	5
			Expected	....	....	14.2	4.7

TABLE V (*Continued*)

EXPERIMENTAL RESULTS FROM THE HYBRIDIZATION OF VARIOUS COWPEA PHENOTYPES, WITH THE GENETIC CONSTITUTION OF THE INDIVIDUALS INVOLVED

Cross 316 { Parents — Clay narrow eye 31K × White 37M F_1 = Black narrow eye
Genotype — NNbbUURRiiEE NNBBUUrrIIEE NNBbUURrIiEE

Generation	Nature of previous generation			Black		Clay		White
	Phenotype	Genotype		Narrow eye	Very small eye	Narrow eye	Very small eye	
F_2 from...	Narrow eye	NNBbUURrIiEE	Actual	11	4	3	1	7
			Expected	11.1	3.7	3	1	6.5
F_3 from...	Black very small eye	NNBbUURRiiEE	Actual	8	...	3	.	...
			Expected	8.2	...	2.7	.	...
Do......	Black very small eye	NNBBUURriiEE	Actual	5	...	...	.	4
			Expected	6.7	...	...	.	2.2
Do......	Clay very small eye	NNbbUURRIiEE	Actual	....	...	2	2	...
			Expected	....	...	3	1	...
Do......	Clay very small eye	NNbbUURRiiEE	Actual	....	...	9	.	...
			Expected	....	...	9	.	...

TABLE V (*Continued*)

EXPERIMENTAL RESULTS FROM THE HYBRIDIZATION OF VARIOUS COWPEA PHENOTYPES, WITH THE GENETIC CONSTITUTION OF THE INDIVIDUALS INVOLVED

Cross 424 { Parents — Wild 01653 × Coffee Taylor 57
Genotype — $NN\overset{\frown}{BT}\overset{\frown}{BT}UURRWWSS$ $nn\overset{\frown}{BT}\overset{\frown}{BT}UURRwwss$

F_1 = Wild $Nn\overset{\frown}{BT}\overset{\frown}{BT}UURRWwSs$

Generation	Nature of previous generation			Black				Coffee			
				Taylor Whippoorwill		Taylor		Taylor Whippoorwill		Taylor	
	Phenotype	Genotype		+S	−S	+S	−S	+S	−S	+S	−S
F_2 from.....	Wild	$Nn\overset{\frown}{BT}\overset{\frown}{BT}UURRWwSs$	Actual	11	4	2	..	3		0	
			Expected	8.4	2.8	2.8	.9	3.7		1.2	
F_3 from.....	Taylor-Whip.	$NN\overset{\frown}{BT}\overset{\frown}{BT}UURRWWSs$	Actual	3	1	....	...	....	....	...	....
			Expected	3	1	...	...	....	....	...	....
Do........	Taylor-Whip.	$Nn\overset{\frown}{BT}\overset{\frown}{BT}UURRWWSs$	Actual	49	14	....	...	14	0	...	....
			Expected	43.3	14.4	....	...	14.4	4.8	...	....
Do........	Taylor-Whip.	$NN\overset{\frown}{BT}\overset{\frown}{BT}UURRWwSs$	Actual	6	2	2	1	....	....	...	....
			Expected	6.2	2.1	2.1	.7	....	....	...	....
Do........	Taylor-Whip.	$NN\overset{\frown}{BT}\overset{\frown}{BT}UURRWwss$	Actual	....	5	....	3	....	....	...	....
			Expected	....	6	....	2	....	....	...	....
F_3 and F_4 from	Taylor-Whip.	$NN\overset{\frown}{BT}\overset{\frown}{BT}UURRWWSS$	Actual	67	....	....	...	....	....	...	....
			Expected	67	....	....	...	....	....	...	....
F_3 from.....	Taylor	$NN\overset{\frown}{BT}\overset{\frown}{BT}UURRwwSs$	Actual	....	....	1	2	....	....	...	....
			Expected	....	....	2.2	.7	....	....	...	....
F_4 from.....	Taylor	$NN\overset{\frown}{BT}\overset{\frown}{BT}UURRWWSS$	Actual	....	....	11	...	....	....	...	....
			Expected	....	....	11	...	....	....	...	....
Do........	Taylor	$NN\overset{\frown}{BT}\overset{\frown}{BT}UURRwwss$	Actual	....	....	....	7	....	....	...	....
			Expected	....	....	....	7	....	....	...	....
F_3 and F_4 from	Coffee-Tay.-Whip.	$nn\overset{\frown}{BT}\overset{\frown}{BT}UURRWwss$	Actual	....	....	....	...	....	14	...	8
			Expected	....	....	....	...	....	16.5	...	5.5
F_4 from.....	Coffee Taylor	$nn\overset{\frown}{BT}\overset{\frown}{BT}UURRwwss$	Actual	....	....	....	...	....	....	...	13
			Expected	....	....	....	...	....	....	...	13

the United States Department of Agriculture, Washington, D.C., where it is available for consultation.

SUMMARY

Seventeen Mendelizing factors of cowpeas were definitely identified. These factors with the characteristic effect they produce are as follows:

A. Seed pod curved after the manner of the *alfalfa* seed pod.
B. *B*rown seed coat.
D. *D*ense speckling, characteristic of the New Era variety.
E. Narrow *e*y*e*.
F. Very *f*ine and dense speckling, giving rise to blue seed coat.
G. Dottin*g*; converts Holstein spots into numerous small ones.
H. *H*olstein type of seed-coat spotting.
I. Eye with *i*ndef*i*n*i*te margin.
L. *L*ongitudinal furrowing of the surface of the seed.
N. Presence of a*n*thocya*n*i*n* pigment factor.
P. *P*ur*p*le seed coat.
R. *R*ed seed coat. (This is the general factor for color, the absence of which determines white seed coat, white flowers, and absence of pigment in vegetative parts.)
S. Black *s*potting on certain types of seed coat.
T. Less dense speckling, characteristic of the *T*aylor variety.
U. B*u*ff, or clay-colored, seed coat.
W. *W*hippoor*w*ill type of seed-coat spotting.
X. Taylor inhibitor cancels (crosses out) the effect of *T*.

The eight factors B, F, N, P, R, TF, U and X, either singly or in combination, give rise to the ten distinguishable seed coat colors, purple, black, dull black, blue, coffee, maroon, buff, red, pink and white. The factors P, B, D, T and F and probably S belong to a linked group. The factors D, T and F restrict the distribution of color pigments in the seed coat. Three independent eye factors I, H and E, either singly or in combination, give rise to the five distinct types of eyes, Watson, Holstein, Small eye, Narrow eye and Very small eye.

Indications were found that when all of the pigment factors are absent, including factor R, there is a tendency for the seeds to be small, weak or abortive.

The flower color has been found to be correlated with the coloration in the seed coat, joints, peduncles, stipules and petioles.

WASHINGTON, D. C.

BACTERIA IN PUFFBALLS *

DELBERT SWARTZ

INTRODUCTION

DURING the past two years, while studying cultures and the spore germination of certain species of Lycoperdaceae collected in the vicinity of Ann Arbor, Michigan, the writer has encountered serious difficulties due to the bacteria which are normally present in the fruit-bodies of these fungi. A survey of the literature in connection with the study of puffballs reveals no mention of bacteria in this connection. Although it has not been possible for the writer to make an exhaustive bacteriological study of these forms, it seemed advisable to present at this time the results of observations that have been made from time to time in connection with the other phases of the work in progress. Let it be said, therefore, that this paper is intended not to give the identity of the bacteria found, but to attempt to present only a general survey of some of the significant facts derived from a continuous observation of them. A brief account of the stains used in the examination of these organisms will be included, and also some notes on their isolation. The latter will show, at least, some important facts regarding the physiology and morphology of the organisms in question. The forms examined will be placed according to the classification of Migula.

THE OCCURRENCE OF BACTERIA IN PUFFBALLS

A study of the fruit-bodies of Lycoperdaceae reveals bacteria under the following four conditions:

1. During the collecting and drying of specimens for future experimentation.
2. In the making of tissue cultures from growing specimens.
3. During spore germination experiments.
4. In single-spore isolations and in attempting to culture pure strains.

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* Paper from the Department of Botany of the University of Michigan, No. 309.

In the fall of 1927 all available species of Lycoperdaceae were brought into the laboratory to supply materials for tissue cultures, and to be dried or matured to provide stock material; this material could then be used for further experiments, such as spore germination, and for other purposes.

When tissue cultures were made from these fruit-bodies, it was soon evident that successful culture depended as much on the condition of the fruit-body as upon the technique of making the culture. The fruit-bodies are naturally dependent upon the conditions under which they have developed. Fruit-bodies growing rapidly under favorable influences were found to be most usable for this purpose, because bacteria are much more prevalent in fruit-bodies growing under conditions unfavorable to rapid development. Water-soaked specimens offer a much more favorable medium for bacterial growth than do specimens which have grown under conditions of less moisture. Hence, fruit-bodies which have had favorable conditions for rapid development would be chosen as the source of clean cultures. A marked rise in temperature and clearing weather after a rainy period are favorable to the drying out of the specimen under natural conditions. This drying out interferes with their becoming soaked through and through. Thus the danger of bacterial invasion is lessened. Tissue removed under aseptic conditions from fruit-bodies which have been subjected to continued periods of wetness usually give rise to cultures which are not free from bacteria. In such instances of bacterial contamination, the fungus can be isolated by placing the culture in the cold room, thus allowing the fungus to outdistance the bacteria. Mycelium may then be removed from the edge of the culture. This mycelium will then give rise to cultures which are bacteria-free. Tissue from fruit-bodies which have not had an excess of rain, and in general have enjoyed more favorable developmental conditions, may be cultivated bacteria-free from the initial culture; but this is by no means true in every instance. From the foregoing facts, it is quite evident that the bacteria present in the growing fruit-bodies of puffballs present considerable difficulty during culture work.

In specimens to be used for herbarium material, and to be studied only from a taxonomic standpoint, the presence of bacteria is of no consequence; in specimens to be preserved dry for cultural studies they are a decided handicap. For the herbarium, the fruit-bodies may be dried in a drying oven without harming them for taxonomic purposes. But when it is desired to study the living spores and their germination, the possible harmful effect of the temperature of the drying oven on the protoplasm of the spore must be considered. Hence it is not advisable to subject them to such a temperature. For this reason the fruit-bodies must be dried differently. They may be placed where the sun's rays have direct contact with them, but this is not always possible. Proper air-drying of such fleshy fruit-bodies is not an easy process, but the following method was found to be fairly satisfactory. The specimens, when collected in the field, are wrapped in relatively clean waxed paper. Upon arrival at the laboratory they are unwrapped, and exposed to the dry air of the laboratory. In the case of large fruit-bodies like the calvatias, this is a slow process requiring considerable care. At the point of contact of the fruit-body and the waxed paper upon which it is drying, there soon results a deposit of moisture from the interior of the fruit-body. This wet spot is followed within a few hours by a discoloration at that point. It is necessary to turn the fruit-body from time to time to insure the exposure of these discolored softening areas to the air. If this is not done, the entire fruit-body becomes a wet mushy mass. This is accompanied by a pronounced putrefactive odor. An examination of the interior of such softened bodies reveals a great number of bacteria. It does not seem that all this activity can be attributed to the bacteria living upon the surface of the fruit-body, or to those which may have fallen upon it from the air. Rather, a considerable part of it, in addition to the possible hygroscopic nature of the tissue, must be due to the bacteria which are on the inside during development. By removing a large fruit-body of *Calvatia gigantea* Batsch to the roof of the Natural Science Building, it was possible to dry it without permanent injury due to bacteria. Repeated turnings of this large specimen were necessary to insure even drying.

In spore germination tests, conducted in the manner described by the author in a previous paper,[1] the presence of bacteria in practically every fruit-body soon becomes very evident. It will not be out of place to review briefly the general method by which the spores of *Lycoperdon pyriforme* Fr. were brought to germination. In this species germination was obtained during experiments in which the spore mass was subjected to alternate wet and dry periods at constant temperature. This constant temperature was somewhat higher than room temperature. Under the microscope few, if any, bacteria are visible in spore suspensions in pure distilled water when the suspensions are first made. However, after a series of wet and dry periods at constant temperature, bacteria become evident. These increase in number according to the time they are subject to these conditions. They must be able to derive enough food from the sterile water and the material extracted from the spore mass for their life-processes and their multiplication. There is no other source of food for them. In the paper on *Lycoperdon pyriforme* referred to, it was stated that this increase in number of bacteria precluded the possibility of using a solid substratum in germination experiments. Bacteria quickly form colonies, and in this way completely obscure the spore mass on such solid substrata. This result was noticed, regardless of whether the medium used was a nutrient medium, or consisted of just plain agar dissolved in water. Of course, this bacterial activity was more pronounced when the substratum contained nutrient material.

Because of this bacterial activity which results when a spray of spores is made upon nutrient agar, the use of such plates is practically impossible. It becomes necessary in this connection to use some substance to inhibit the growth of the bacteria, and yet not interfere with the activities of the fungus spore. These conditions are hard to supply. If, as in the case of *Lycoperdon pyriforme*, bacteria have made the study of spore germination difficult at the end of the minimum time of six days, this examination is much more difficult when the minimum time is considerably longer. It is much easier in case sterile water alone has been used. The difficulty is increased when a spray of germinating spores in this distilled water is made upon a nutrient agar plate.

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[1] "Spore Germination of *Lycoperdon pyriforme*," *Pap. Mich. Acad. Sci., Arts and Letters*, 9 : 299–304.

EXPERIMENTAL WORK

In order to study the types of bacteria which could be isolated from various fruit-bodies, isolations were made from the fruit-bodies in the writer's collections. For these isolations agars were used. A bacterial agar was made as follows: 3 gm. beef extract, 10 gm. peptone, 15 gm. agar in 1000 c. c. distilled water. A maltose agar was also made: 5 gm. maltose, 0.1 gm. peptone, 0.5 gm. $MgSO_4$, 0.5 gm. $CaNO_3$, 0.25 gm. KH_2PO_4, 15 gm. agar in 1000 c. c. distilled water. Isolations were made on these two agars and run in parallel series during the course of the experiment. The fruit-bodies used belonged to the following species:

Lycoperdon pyriforme Fr.
Lycoperdon gemmatum Batsch.
Calvatia saccata (Fr.) Lloyd.
Calvatia caelata Bull.
Calvatia cyathiformis (Bosc.) Morg.
Bovista plumbea Pers.

Of each of these species two fruit-bodies were used, one of which had matured and opened under habitat conditions before being collected and brought into the laboratory. The other had not reached full maturity at the time of collection, and was brought into the laboratory to mature. None of these latter specimens had visible breaks in the peridium.

Three methods were used to make isolation plates of the bacteria: (1) dilution method (as used by bacteriologists in milk and water analysis); (2) spray method; (3) smear method. In making these dilutions and later subcultures, the usual precautions against contaminations were taken.

When bacterial colonies appeared on the plates successive transfers were made until pure cultures were obtained. Successful isolations were obtained as follows:

CULTURE NO.	SOURCE	METHOD
177 a	Opened Bovista plumbea	Smear
154 a	Unopened Bovista plumbea	Spray
146 a	Unopened Calvatia cyathiformis	Spray
171 a	Opened Calvatia cyathiformis	Smear
134 a	Opened Lycoperdon pyriforme	Dilution
137 a	Unopened Calvatia caelata	Dilution
154 b	Unopened Bovista plumbea	Spray
176 b	Unopened Lycoperdon pyriforme	Smear
136 a	Opened Lycoperdon gemmatum	Dilution

Numbers refer to number of isolation plate.
a = first isolation from dish
b = second isolation from dish

From this list, which is made from the first group of isolation plates that were set up, it is evident that bacteria may be isolated from opened or unopened fruit-bodies. There were other bacterial colonies on the isolation plates, but these grew weakly and failed to survive subsequent transfers. Lack of time has prevented the cultural study of these additional forms on special nutrients. The significant fact brought out by the list is that bacteria are normally present in puffballs, i.e., in all the genera which have come within the limited scope of this report. It does not seem possible that such a general presence as herein shown could be traceable to chance contaminations. Moreover, there is a suggestion of more than a chance relationship when it is remembered that this association is a common one. Further, this general occurrence offers a considerable field for speculation, both as to how the bacteria may gain entrance, and at what stage in the development they ordinarily enter. This will be referred to again. Let us now turn to the description and discussion of the various types of organisms which have been isolated.

DISCUSSION AND DESCRIPTION

The bacteria isolated from the fruit-bodies of Lycoperdaceae are all Cocci and Bacilli. The coccus forms are in some cases grouped together in Sarcina-like groupings. An exception to this is a form of Streptococcus. The individual cocci of this Streptococcus are somewhat larger than the ordinary described forms. The bacilli are both large and small forms. Further details will be brought out in the descriptions that follow. On slides of spores that are undergoing the treatment essential to germination, involution forms of these bacteria are often to be seen. In all the slides prepared from the colonies of these organisms after they had been isolated and were growing on a nutrient agar, there were no examples of involution forms. This indicates that the optimum growth conditions are more nearly supplied by the nutrient than by the distilled water, or by the spore extract on the germination slide.

Certain observations have been made of each of the organisms given in the list in the preceding section. The results of these more detailed observations follow, and include a description of the growth in broth, on bacterial agar and maltose agar. In addition motility has been determined; oxygen relations have also been ascertained. Two stains have been used: (1) 1 per cent aqueous solution of gentian violet; (2) Ziehl-Neelson's carbol fuchsin.

I — 134 a. Long rods, occurring singly, in pairs, or in chains of from 3 to 12 individuals. Spores formed in large numbers in old cultures. Rods motile, aërobe and facultative anaërobe,[2] growing best at room temperature.

Broth. — Heavy precipitate formed in 36 hours.

Bacterial agar. — Growth much spreading from the track of the inoculation needle, dirty whitish, glossy, moist, elevated and translucent. Edge of the colony very irregular on the surface of the medium.

Maltose agar. — Growth much more limited than in bacterial agar; confined to the track of the needle. Appears watery on the surface of the medium. This medium is less favorable than bacterial agar.

Source. — The interior of a fruit-body of *Lycoperdon pyriforme*, which was fully mature when collected.

II — 176 a. Long rods, occurring in chains, rarely singly. No spores formed. Non-motile aërobe growing best at room temperature.

Broth. — Precipitate formed which settles in 24–36 hours.

Bacterial agar. — There is a marked tendency toward the formation of separate individual colonies scattered over the surface of the slant. Colonies are round, gray, translucent and easily separable from the medium.

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[2] In the study of this organism and the others which follow anaërobic conditions were supplied by the removal of the oxygen by a mixture of potassium hydroxide and pyrogallic acid.

Maltose agar. — Essentially the same characteristics as shown on bacterial agar.

Source. — Interior of an unopened fruit-body of *Lycoperdon pyriforme.*

III — 146 a. Small coccus forms grouped in Sarcina-like groupings. Aërobe, non-motile, growing best at room temperature.

Broth. — Very slight cloudiness after 36 hours.

Bacterial agar. — Very feeble growth, closely confined to the needle track. Whitish and translucent.

Maltose agar. — Essentially the same as on bacterial agar.

Source. — Interior of an opened fruit-body of *Calvatia cyathiformis.*

IV — 171 a. Short, rather thin rods, occurring singly or in pairs, very rarely in chains. Motile, no spores, aërobe growing best at room temperature.

Broth. — Very dense precipitate formed within 36 hours. The surface of the broth is completely covered with a film.

Bacterial agar. — Smooth, glistening growth, yellow pigment, closely adhering to the track of the needle, and growing very sparsely.

Maltose agar. — Characteristics as in bacterial agar, but evidently not as favorable to the organism.

Source. — Interior of an opened fruit-body of *Calvatia cyathiformis.*

V — 154 b. Streptococcus, 4–12 cocci in chain, non-motile, aërobe, and growing best at room temperature.

Broth. — Cloudy after 36 hours.

Bacterial agar. — Very scant growth, spreading slightly from the needle track, translucent, dirty whitish, and showing a few isolated, separate, round colonies.

Maltose agar. — Growth less than in bacterial agar; otherwise the same.

Source. — Interior of an unopened fruit-body of *Bovista plumbea.* Both peridia of this fruit-body were unbroken when the spore suspension was made.

VI — 177 a. Small rods, occurring singly or in pairs, very rarely in chains; no spores, motile, aërobe, and grows best at room temperature.

Broth. — Very heavy precipitate formed after 36 hours. The entire surface of the broth is covered with a film.

Bacterial agar. — Growth luxuriant, with a somewhat denser wrinkled central portion extending the length of the colony. This dense central portion is fringed by a much less dense area. Growth slow, dirty whitish, translucent mass. A few separate isolated colonies are formed.

Maltose agar. — Closely confined to the track of the needle; otherwise the same as bacterial agar.

Source. — Interior of an opened fruit-body of *Bovista plumbea.*

VII — 154 a. Coccus, grouped as in Sarcina. Non-motile, aërobe, and grows best at room temperature.

Broth. — Very slight cloudiness after 36 hours.

Bacterial agar. — Very scant growth, confined to the track of the needle; whitish, glistening and translucent.

Maltose agar. — Essentially the same as bacterial agar.

Source. — Interior of an unopened fruit-body of *Bovista plumbea.*

VIII — 136 a. Small cocci, apparently without definite grouping. Non-motile, aërobe, growing best at room temperature.

Broth. — Slight cloudiness after 36 hours.

Bacterial agar. — Growth very slow, limited to the needle track; glossy white and translucent.

Maltose agar. — Very scant growth. Otherwise the same as bacterial agar.

Source. — Interior of an opened fruit-body of *Lycoperdon gemmatum.*

These notes have been taken from cultures and stained preparations of bacteria which were isolated from the interior of the fruit-bodies of the puffballs. In addition to those listed and described above, there were other bacteria evident as pin-point colonies on the first isolation plates. These failed to withstand subsequent transfers. Successful isolations and studies of these could doubtless be made, if special nutrients were devised for them.

POSSIBLE SOURCES OF BACTERIA

Such a general occurrence of bacteria in these fruit-bodies naturally brings up the questions how and when the bacteria may enter the fruit-body. In view of the conditions under which these fungi grow and mature in their natural habitat, it is not surprising that certain types of saprophytic bacteria are to be found on the exterior of the fruit-body. Coming up through and growing for some time among old leaves, twigs and the like on the forest floor, the fruit-body could easily come into contact with many types of bacteria — those living on the forest débris as well as those that normally are found in the soil. This possibility is more evident if one considers that the surface of the fruit-body is ordinarily moist, and often carries some organic matter with it. In addition to the forms mentioned above, the bacteria of the air could come into contact with and lie upon the surface of the fruit-bodies. Such organisms of the air can, of course, fall upon the fruit-body at any time during its development. Other bacteria living upon any host whatsoever in the woods, or wherever the puffball happens to be growing, could fall upon the surface of the fungus. This makes such organisms potential sources of contamination at any time. In addition to these possibilities, bacteria may be carried to the fruit-body by insects which happen to come into contact with it. The grubs which burrow into the interior may carry bacteria with them. The burrowing of the grubs through the exoperidium leaves a possible portal of entry for the bacteria which otherwise could not enter. Such insects must play an important part in the spreading of bacteria through a given host range. The smaller animals sometimes feed upon these fruit-bodies and thus contaminate them. This whole group of agents can possibly account for the supply of bacteria to the surface of the fruit-body, or for bacteria that may be found where the peridium has been eaten into or broken. However, these agents, in the opinion of the writer, do not sufficiently explain the extensive presence of bacterial organisms in the interior of the fruit-body when the peridium (or the peridia, as the case may be) is still intact. It is necessary to look for other explanations. It is quite evident from a developmental study of certain species that an invasion of bacteria into the stalk during early developmental stages may explain their later presence in the interior fertile regions. The elongation of the hyphae of the stalk into that region might carry them along. This, however, does not explain their presence in those fruit-bodies which show no trace of a rupture in the peridium of the stalk. It is indeed difficult to account for their presence when there are no macroscopic evidences of such a break in the peridium at any point.

The possibility that bacteria may gain entrance into the interior of the fruit-body as the result of repeated water-soaking does not seem plausible. Ordinarily living organisms are so constructed that they are able to resist the invasion of saprophytic organisms. It cannot logically be expected that the fruit-bodies of these fungi are so markedly different in this respect from the other forms of plant life. This must be true even in cases of extended periods of water-logging. This does not suffice as a possible explanation. The effect of drying after wet conditions such as those mentioned above may cause minute openings in the peridium through which bacteria could be washed by subsequent rains. This will not account for the presence of bacteria in fruit-bodies such as those of the Bovista treated in this paper. In the case of this fungus, there is a heavy outer peridium present through most of the developmental stages. This outer peridium sloughs off at maturity, leaving only the soft, leathery inner peridium to protect the capillitium mass. One of the fruit-bodies of this genus still had both of these peridia intact. No possibility already given seems adequate to explain the presence of bacteria in such a fruit-body. It becomes quite evident that the status of our knowledge of the subject does not permit of a satisfactory answer to the question how bacteria gain entrance into a fruit-body during its development. There is still to be considered, however, the beginning stages of fruit-body development. The problem immediately arises concerning the possibility of the bacteria becoming associated with the hyphae at the very first stage of the development of the fruit-body. The material at hand does not lend itself to the solution of this question. The entire problem must, therefore, be left unsolved.

SIGNIFICANCE OF BACTERIA IN THIS CONNECTION

It is purely speculation if one attempts to attribute any significance to the bacteria in the fruit-body. Is there a relationship other than ordinary saprophytism? Is this relation symbiotic? Are bacteria necessary to the breaking down of the capillitium during the ripening process? It is quite evident that conditions within the fruit-body are favorable to bacterial growth at certain times. These conditions would lead to the presence of bacteria occasionally, but do not explain the presence of bacteria in unopened fruit-bodies which have all the protective coverings intact. There is no evidence at hand for or against symbiosis or parasitism. The organisms can be just as easily considered casual saprophytes. There has not been sufficient work done to show a constant relationship of a certain type or species of bacteria to a particular species of puffball.

SUMMARY

Bacteria have been consistently found in puffballs at different periods during their development.

Bacteria are present in fruit-bodies with either broken or unbroken peridia.

Eight examples of two morphological forms have been isolated.

These forms were cocci and bacilli.

The relationship of these bacteria to the fruit-body or puffballs is not undertsood.

The writer wishes to express his thanks to Dr. C. H. Kauffman for suggestions and criticisms during the preparation of this paper.

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MONTANA MOSSES FROM THE FLATHEAD NATIONAL FOREST *

FRANCES J. THORPE

THE mosses listed in this paper were collected by Dr. C. H. Kauffman in the course of an expedition to western Montana for the purpose of studying and collecting the flora, both phanerogams and cryptogams, for use in the University of Michigan Herbarium. On arrival at Kalispell, Montana, which lies in the rich agricultural valley north of Flathead Lake, the party of two, through the unexampled kindness of Supervisor Lloyd Hornby of the Flathead National Forest, was provided with all the facilities for botanizing that one could ask for. Quarters were provided at the Echo Lake Ranger Station at the foot of the Swan Range, thirty miles from Kalispell. The place is surrounded by extensive forests and easy horse trails lead into the mountains. Horses were supplied and meals obtained at the Ranger Station. The courtesies and helpfulness of the ranger, Mr. J. E. Thompson, made it possible to gather the large amount of material which was brought back to Ann Arbor. The party stayed from June 26 to August 21, 1928, sometimes working on one group of plants, sometimes on a different one, depending on the seasonal or weather effects on the content of the flora.

The mosses in this region are extremely abundant. On the gently sloping or flat areas at the foot of the ridge and extending well upward along the numerous streams, wherever it was heavily forested, rocks, logs, humus and stream beds were literally covered by a continuous mass of mosses and liverworts. This type of country was easily accessible, much of it being within a few minutes' walk, with excellent trails leading far beyond. At higher altitudes, about 4000 feet, not only the moss flora but the entire

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* Paper from the Herbarium of the University of Michigan, No. 11.

flora underwent rapid changes to different species of plants. On the bare, rocky slopes of the mountains, adjacent to subalpine meadows, where in July deep snow beds were still prominent on the north side, most interesting moss collecting was possible. By collecting at intervals of several weeks, mature sporophytes could be readily obtained. The heavy and continuous rains through later June and July kept the Bryophytes all over this region in a remarkably fine and impressive condition.

The collection of mosses from this region is of great interest because of the number of different fruiting specimens obtained in the limited time and because of the fact that Montana is a region little explored by bryologists. The list of mosses is here increased by twenty-three species or varieties which do not appear on the lists published before this time. Several of these are unusual forms and a few differ in some respects from the descriptions given in the various manuals. Thirty-seven genera are represented, and sixty species and varieties. The specimens were all collected in July above 3300 feet altitude and most of them were growing between altitudes of 4500 feet and 7000 feet. Subalpine forms are then to be expected. Rock-growing forms are quite numerous also; at least a third of the total number were found on rocks and boulders. Ten species are confined to the northwest portion of the United States and Canada; most of these are reported from high altitudes of this region only.

Two lists of Montana mosses had been published prior to 1910. Since then only scattered records of a few species have been noted. The first list occurs in a bulletin prepared by Wilson P. Harris and Carolyn W. Harris (8), based on material collected during 1901, and, with a few additions, published in 1904. Thirty-seven species representing nineteen genera with data on locality, altitude and time of collection — and frequently the habitat — appear in this list. The collecting was done during the months of June, July and August. The elevations at which mosses were collected range from 2700 feet to 3800 feet, with the majority noted as growing below 3300 feet, where there is usually the forested plain or the foothills of the mountains in the region covered. The other publication listing Montana mosses is *Montana Botany Notes* (10), by Marcus E. Jones, which appeared in 1910. This has a section devoted to the moss flora, and the list given includes the list of the Harris collection, the species collected by Dr. John M. Holzinger in July, 1898, and a number of species collected by Mr. Jones himself. The total number of species and varieties is about two hundred. An account of the region through which Dr. Holzinger collected, with descriptions of thirteen species, heretofore undescribed or new to North America, is quoted from a paper which appeared in the *Botanical Gazette* of August, 1900. Mr. Jones gives briefly the region covered by Mr. Harris and states that he himself collected the more common mosses around Flathead Lake and from the adjacent mountains.

Mr. Holzinger collected entirely within a region about ten miles in radius from the upper end of Lake McDonald, now in Glacier National Park. No altitudes are given, however. The region covered by him is some fifty miles farther north than the upper end of the area described by Mr. Harris, who collected from around Missoula, and north to the upper end of Flathead Lake, then into the mountains northeast of the lake up to about 3300 feet elevation. Only one specimen is mentioned on his list as growing above 3300 feet — *Eurhynichium strigosum* B. & S. at 3800 feet.

The mosses reported in this list were collected by Dr. Kauffman in the mountains east of Echo Lake, the majority at about 4000 to 7000 feet altitude. Twenty-three species and varieties do not appear in the lists previously published.

A more detailed description of this general region and of the region immediately surrounding the Echo Lake Ranger Station, which was used as a base during the collecting, is given in a paper on "Montana Discomycetes from the Flathead National Forest," by G. B. Cummins, which appears in this volume (pp. 105–115). There is an account of this general region of the Swan Range on pages 153–155 of a pamphlet by M. J. Elrod, entitled *A Biological Reconnoissance in the Vicinity of Flathead Lake,* published as Bulletin No. 10 of the University of Montana Biological Series No. 3, 1902.

The nomenclature of mosses adopted by V. F. Brotherus, as given in Engler and Prantl's *Die natürlichen Pflanzenfamilien*, Volumes 10 and 11, has been followed in this paper. The habitat of each species is given with the comparative altitude at which it was collected. Sometimes additional notes on the particular specimen, or on general distribution, are added. The specimens which comprise this collection are in the Herbarium of the University of Michigan. A few other specimens of Montana mosses appear in this Herbarium also, most of them included in Fascicles 1 to 26 of Dr. Holzinger's exsiccati. Dr. George B. Kaiser reports several scattered specimens from Montana in the Sullivant Moss Society Herbarium at Philadelphia, but says that no comprehensive collection has been made since 1910. Duplicates of Mr. Harris's collection are at the New York Botanical Gardens and at the University of Montana.

For verification of some of my identifications and for assistance in determining several difficult specimens, grateful acknowledgement is made to Dr. George B. Kaiser, Dr. John M. Holzinger and Dr. A. J. Grout.

LIST OF SPECIES

In this list an asterisk (*) indicates species that have not appeared in previous lists.

AULACOMNIUM PALUSTRE L. — On soil in a mat of *Campylium stellatum* (Schreb.) Bryhn., 3500 feet, July, 1928.

*BRACHYTHECIUM ACUTUM (Mitt.) Sulliv. — On soil and rotten logs in moist places, 3300 feet, July, 1928. An uncommon species usually found in the northern latitudes; the type specimen is from British Columbia. Grout gives its distribution as "Northern United States and Canada, across the continent; south to New Jersey, Ohio, and Colorado."

*BRACHYTHECIUM FLEXICAULE R. & C. — On bark of a rotting tree trunk, 3500 feet, July, 1928. Dr. Brotherus gives this as an eastern form only, but Grout (7, p. 31), notes that a specimen from Revelstoke, B. C. (Macoun), growing on earth, was distributed as *B. glareosum* B. & S.

BRACHYTHECIUM STARKEI (Brid.) B. & S. — On wet rocks, 3300 feet, July, 1928. This specimen was traced to *B. oedipodium* Mitt., in Lesquereux and James' manual, but Grout in his monograph places all *B. oedipodium* specimens in *B. Starkei* and Brotherus does not include *B. oedipodium* as a good species.

*BRACHYTHECIUM VELUTINUM B. & S. — On banks along trail, 4500 feet, July 29, 1928. A sterile specimen whose vegetative characters place it in this species. This moss is collected in mountainous regions of the north with but few exceptions.

*BRYUM INTERMEDIUM Brid. — On gravelly humus in open places, 3500 feet, July, 1928. Near *B. caespiticium* L., but usually growing in moister places.

BRYUM LUCIDUM E. G. B. — On moist earth along trails of the forest, 4500–5000 feet, July 29, 1928. At first glance this fine large moss would readily be taken for a Mnium, but the long slender capsule with the neck distinct and the short wide cells of the leaves place it at once in the genus Bryum. Mrs. Britton (2, p. 53) first described this plant in 1891. It is near Rhodobryum, but "differs in habit, size, leaves not twisted when dry and pedicels single," according to her description. She also says that the moss is light glossy green. The specimen in this collection differs from the original description in being a rather dark green, with leaves twisted spirally around the stem in a loose manner or at least with leaves twisted one-half turn on some of the plants. The plants measure from 3 to 5 cm. in height, and the pedicel 4 to 4.5 cm. Both setae and outer peristome are exceedingly brittle. The teeth of the outer peristome show the blunted end as noted in Mrs. Britton's drawing (2, p. 57), but the upper one third of each tooth is strongly papillose with numerous small papillae and is quite different from the lower part. An annulus is plainly present. This species was collected by Dr. Holzinger in Glacier National Park.

*BRYUM TURBINATUM (Hedw.) Schwaegr. — On wet clay soil, 4500 feet, July, 1928. A rare species reported from only a few places in the United States. The male plants are very slender and in separate tufts or mixed with the fertile ones. The perigonium is in a tuft of a few leaves.

*BUXBAUMIA INDUSIATA Brid. — On a very rotten log among thin mosses and liverworts, 4000 feet, July 31, 1928. Reported in Engler and Prantl from British Columbia only on our continent, although Dr. Grout says it is probably quite widely distributed over the United States, but not often collected. It is a moss of mountainous regions and much rarer than *B. aphylla* L. It is reported by Mrs. Britton (2, p. 49) as collected by Mr. John B. Leiberg in Idaho.

CALLIERGON SCHREBERI Willd. — On humus, 4000 feet, July 31, 1928. Sterile. The species produces capsules sparingly.

*CAMPYLIUM STELLATUM (Schreb.) Bryhn. — On humus, 3500 feet, July, 1928. A slender form, with prostrate stems, var. *protensum*, was reported by Holzinger.

CATHARINAEA SELWYNI (Aust.) Kindb. — On humus and clay, 3500 feet, July, 1928. A few plants with sporophytes were in a mat of *Campylium stellatum*. The species is collected only in the northwestern part of North America, according to Brotherus (3, p. 494).

CERATODON PURPUREUS (L.) Brid. — On burned-over ground, at various altitudes, July 29, 1928.

*CLAOPODIUM LEUCONEURUM Sulliv. & Lesq. — On moist rock, 4000 feet, July, 1928.

*CLAOPODIUM WHIPPLEANUM Sulliv. — On rock, 4500 feet, July, 1928. (The genus Claopodium is closely related to Thuidium, but the very short, broad capsule distinguishes it without the use of a lens. In North America it is reported from the West and Northwest only — from British Columbia to California and as far east as Idaho. Four different species occur in this country, two of which were collected by Dr. Kauffman. Dr. Holzinger collected *C. Bolanderi* Best from farther north in the state. Dr. Brotherus states that *C. leuconeurum* may be a depauperate from of *C. Whippleanum*, but there are enough points of difference for both to be given specific rank in Engler and Prantl. *C. leuconeurum* has smooth setae, annulus, and three short cilia between the teeth of the peristome, but *C. Whippleanum* shows a decidedly rough seta, no annulus, and but two cilia present. The latter moss has been reported only from California before.)

*DICRANOWEISIA CRISPULA (Hedw.) Lind. — On sides of rocks, Aeneas Lake, 5200 feet, July 21, 1928. Mixed with Pseudoleskea. A western moss of high altitudes.

DICRANUM BONJEANI De Not. — On rocks at 3500 feet, July, 1928.

*DICRANUM BONJEANI De Not. var. BREWERIANUM Lesq. — On rocks and logs, 5000 feet, July, 1928. The variety is found only in the mountains. It differs from the typical form in having narrower leaves, which are scarcely undulate, and much more slender stems. The cells are also longer.

DICRANUM FUSCESCENS Turn. — On rotting wood, 3200–5000 feet, July, 1928. Seldom collected below 1000 feet.

*DICRANUM MIQUELONENSE Ren. & Card. — Covering large rock, 4000 feet, July 28, 1928. No capsules. Answers the description as given in the *Botanical Gazette,* 14 : 93, except that some of the leaves are a little longer. "Fruit unknown."

*DIDYMODON RUBELLUS (Hoffm.) B. & S. — On base of tree mixed with *Eurhynichium strigosum* var. *robustum.* 3300 feet, July, 1928.

DISTICHIUM CAPILLACEUM B. & S. — In compact mats with sterile strands of *Hypnum sp.,* growing in crevices of boulders, Aeneas Lake, 5200 feet, July 21, 1928.

DREPANOCLADUS UNCINATUS (Hedw.) Warnst. — On rotten wood, 4500 feet, July, 1928. Common in subalpine regions, but variable and usually growing on stones or soil.

*EURHYNCHIUM STRIGOSUM (Hoffm.) B. & S. var. ROBUSTUM Roell. — On wet rocks by stream, 4000 feet, July 31, 1928. The species was reported by Holzinger.

FUNARIA HYGROMETRICA (L.) Sibth. — Frequent on various kinds of soil and burned wood, 3000–6000 feet, July 29, 1928.

GRIMMIA PATENS (Dicks.) B. & S. — On large flat rock, 4500 feet, July 12, 1928. A distinct species with a curious double wing on the back of the nerve of the leaf. Not common.

HEDWIGIA ALBICANS (Web.) Lindb. — On rocks and rock ledges, 6000 feet, July 24, 1928.

HYGROHYPNUM PALUSTRE (Huds.) Loeske. — On wet rock by stream, 5000 feet, July, 1928. A variable moss with many alpine forms.

HYLOCOMIUM PROLIFERUM (L.) Lindb. — On humus in moist forest, 3500 feet, July 31, 1928. Common in the north and west.

LEPTOBRYUM PYRIFORME (L.) Wils. — On a burned, decaying tree trunk, 4500 feet, July 29, 1928.

*MNIUM DRUMMONDII B. & S. — On humus in moist woods, 3500 feet, July, 1928. Infrequent. Slightly similar to *M. affine*, but the leaves are serrate in the upper one half only and the teeth consist of one much elongated cell. A northern species.

MNIUM MARGINATUM (Dicks.) Palis. — On humus along streams, 3000 feet, July, 1928. Because of the dark brown mouth of the capsule this resembles *M. spinulosum* superficially. Found only in northern latitudes.

MNIUM ORTHORRHYNCHUM Brid. — A few strands only in a mat of *Claopodium Whippleanum* on a rock, 4500 feet, July, 1928. A moss of cool or elevated regions.

MNIUM SPINULOSUM B. & S. — On moist bank of stream in pine woods, 4800 feet, July 29, 1928. Common in mountain regions.

*MNIUM SUBGLOBOSUM B. & S. (?) — In wet woods on soil, 4000 feet, July 31, 1928. Sterile. This moss is confined to the woods of northwest America and is rare there, according to Dr. Brotherus. It differs from the rather common *M. punctatum* in its bisexual flowers and "in its broadly obovate leaves, not emarginate nor apiculate at the apex," and in the uniform green color of the margin, formed of two or three rows of long cells one layer thick, which is usually brownish in *M. punctatum*. The specimen in this collection does not agree entirely with either the typical form of *M. subglobosum* or any of the varieties described. Many of the leaves are slightly indented at the apex and a few are very obscurely apiculate. Since the specimen is sterile it can be placed here only on the basis of the vegetative characters shown.

NECKERA MENZIESII Hook. — Hanging from the under side of a large rock, 4500 feet, July 29, 1928. This is a local species collected only in western North America from Alaska to California. The curious long lateral filiform flagellae make a growth of this moss appear as if two species were intertwined.

ORTHODICRANUM STRICTUM Schleich. — On decayed logs, 3000–3300 feet, July 28, 1928.

*ORTHOTRICHUM CUPULATUM Hoffm. — On dry rocks at high elevations, 6000 feet, July 24, 1928. Mixed with *Hedwigia albicans.* Confined to high altitudes of the United States and rather rare, according to Dr. Brotherus (3, Bd. 11, p. 17). Not collected in the East at all (6, p. 181).

ORTHOTRICHUM SPECIOSUM Nees. — On branches of dead conifers in abundance, 4000 feet, July 11, 1928.

PLAGIOTHECIUM DENTICULATUM B. & S. — On humus, 4000 feet, July, 1928.

PLAGIOTHECIUM ELEGANS Hook. — On rotting wood, 4800 feet, July 29, 1928. This specimen has alar cells slightly enlarged, but otherwise it agrees with the description in the manual of Lesquereux and James. Its usual habitat is given as crevices of shaded rocks or soil.

*PLAGIOTHECIUM PULCHELLUM B. & S. — On roots of trees, 4000 feet, July, 1928.

PLAGIOTHECIUM SYLVATICUM (Huds.) B. and S. — On humus, 4000 feet, July, 1928.

POLYTRICHUM JUNIPERINUM Willd. — On soil on top of overturned tree roots, 5000 feet, July 31, 1928.

*POLYTRICHUM JUNIPERINUM Willd. var. ALPINUM Schimp. — On dry soil, 6500–7000 feet, July 15, 1928. This is collected in high mountains only. It is shorter in every way than the species and has a smaller capsule.

POLYTRICHUM PILIFERUM Schreb. — On ledges of dry slopes, 5000 feet, July, 1928.

*POLYTRICHUM PILIFERUM Schreb. var. HOPPEI Rabenh. — On rocks and sandy barren ground, 6500–7000 feet, July 15, 1928. A mountain variety easily identified by the almost square orange capsules erect on the seta.

PSEUDOLESKEA RIGESCENS Lindb. — On rocks and trees, Aeneas Lake, 5200 feet, July 21, 1928. This is an alpine or subalpine moss showing variations due to habitat. The rock-growing specimen is much more slender than the tree-growing one. It has been reported from British America.

PTILIUM CRISTA-CASTRENSIS (L.) De Not. — On humus in deep woods, 3800 feet, July 3, 1928.

RHACOMITRIUM CANESCENS (Timm.) Brid. — On rocks, 4500 feet, July, 1928. All but one of the species of this genus are alpine or subalpine and local in mountain districts. This species is distinguished from all others by having cells of the leaf strongly papillose on *both* sides. It is confined to the northern part of North America (3, Bd. 10, p. 314).

RHYTIDIADELPHUS TRIQUETRUM (L.) Warnst. — On humus in woods, 4000 feet, July 31, 1928.

RHYTIDIOPSIS ROBUSTA (Hook.) Broth. — On humus, 4000 feet, July 31, 1928.

*SCLEROPODIUM OBTUSIFOLIUM (Hook.) Kindb. — On wet stones, 3800 feet, July, 1928. Reported only from western United States and British Columbia. It seldom fruits.

TETRAPHIS PELLUCIDA Hedw. — On decayed wood, 3300 feet, July, 1928.

TIMMIA MEGAPOLITANA Hedw. — On moist bank under overhanging tree trunk, 4000 feet, July 31, 1928. Found only in the Rocky Mountains and northward, according to Grout (6, p. 199), who states that the moss usually collected in the eastern states and called *T. megapolitana* is probably *T. cucullata*. Dr. Brotherus does not give *T. cucullata* as a separate species.

TORTULA RURALIS (L.) Ehrh. — On dry granite rock, 4800–6000 feet, July 29, 1928. Especially common in the Pacific northwest.

*TRICHOSTOMUM CYLINDRICUM (Bruch) C. Mull. — On clay soil, 4500–6000 feet, July 28, 1928. Usually found in hilly or mountainous districts (9, p. 94).

*WEBERA NUTANS Hedw. — On soil and rotten logs, 3300–4800 feet, July 29 and 31, 1928.

WEBERA CRUDA (L.) Bruch. — In rock crevices, 5000 feet, July 31, 1928. An infrequent alpine and subalpine species.

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STUDIES ON THE RÔLE OF THE HOST IN THE GENUS DIAPORTHE *

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IN SUCH fungi as the species of Diaporthe and related genera, the morphological characters used for classification are often a composite of fungous and host tissues, and it is easily conceivable that different hosts or different environmental conditions due to variation in the physical or chemical composition of the substratum might result in varying morphological characters for one and the same fungus, particularly so when we realize the variability of stromatic formations. This statement is true of species occurring on a variety of hosts. On the other hand, it has long been known that many species of Diaporthe, as well as of other sphaeriaceous genera, are quite distinctly limited to certain host genera or species under natural conditions. It has been the custom in the past to describe as new any form occurring on a new host, even though it be only slightly or not at all morphologically distinct from previously described species on other hosts. In view of these facts it becomes increasingly important, in the study of the genus Diaporthe and many other similar genera which occur saprophytically or perhaps semiparasitically on numerous host genera, to understand the rôle played by the host in the morphology and the biology of the fungus. Related species apparently limited as to host in nature can often be grown on a wide variety of dead twigs in culture. In such species the question arises whether the morphological variations are caused by the different host tissues or whether they represent specialized species limited to certain hosts, as in the case of many parasites. Certain results given below seem to indicate that, in some cases at least, the latter alternative is true. It is undoubtedly true that

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many species of Diaporthe and related genera begin their life-histories as weak parasites and produce the perithecial stage after the host twig has been killed. The frequent occurrence of conidial stages on still living twigs, often back from the killed tips bearing perithecia, indicates this. In some cases the parasitism of the conidial stage has been definitely established, as in *Diaporthe phaseolorum* (C. & E.) Ell. (7), *Diaporthe batatatis* Hart. & Field (8) and *Diaporthe Citri* Wolf (6 : 17).

A most interesting, closely related group of species of the genus Diaporthe is that found on species of the host genus Acer. These species differ slightly in certain morphological characters and appear to be limited to certain host species, as follows:

Diaporthe pustulata (Desm.) Sacc., occurring on *Acer pseudoplatanus* L., has limited, isolate entostromata with definite ventral zones, and they often appear on the surface as definitely outlined by a raised marginal ridge. The spores are 12–15 × 3–5 μ.

Diaporthe varians (Curr.) Sacc. on *Acer campestre* L. has isolate to pustulate-effuse stromata, a definite ventral zone and inequilateral ascospores 13.5–19 × 4–6.5 μ.

Diaporthe dubia Nit., occurring on *Acer saccharum* Marsh., *A. saccharinum* L. and *A. negundo* L., has isolate to pustulate-effuse stromata, the ventral zones of which are usually lacking or incomplete (Pl. XXXIV, Fig. 7). The ascospores (Pl. XXXIV, Fig. 8) of this species are straight and measure 13–16 × 4–7 μ. The asci (Pl. XXXIV, Fig. 9) are 60–73 × 10–12 μ.

Diaporthe acerina (Pk.) Sacc. on *Acer spicatum Lam.* usually has widely pustulate-effuse stromata with a definite ventral zone (Pl. XXXIV, Fig. 1). The ascospores (Pl. XXXIV, Fig. 2) are straight and measure 12–15 × 4–5 (5.5) μ. The asci (Pl. XXXIV, Fig. 3) are 60–70 × 7–10 μ.

The two American species, *D. acerina* and *D. dubia,* of the foregoing group, have been compared in culture as given below.

DIAPORTHE ACERINA (Pk.) Sacc.

Material of *Diaporthe acerina* (Pk.) Sacc. collected on twigs of *Acer spicatum* Lam. at Economy Lake, Colchester Co., Nova Scotia, and identical with the type of Peck's *Valsa acerina* (N. Y.

St. Mus., Indian Lake, July, 1874), was used as a source for single ascospore cultures. Type material (N. Y. St. Mus., Fl. N. Y., Catskill Mts., by Peck, July) of *D. Peckiana* Sacc. (*Nuov. giorn. bot. ital.*, n. s. 23 : 187) and of *Valsa albo-cincta* Cke. & Pk. (Kew Herb., Herb. M. C. Cooke No. 317) (1, p. 120) show these species to be synonymous with *D. acerina.*

Ascospores from twigs kept in a damp chamber from three to four days germinated within twenty-four hours after being sprayed on agar. The germinating spores measured 12–13 × 5.5 μ and produced a single germ tube 5.5 μ in diameter.

On oatmeal agar, scattered, superficial, hemispherical to confluent, pycnidial stromata, 0. 2–3 mm. in diameter, were formed. The larger of these were often sterile. Spherical to irregularly flattened locules were formed in many of the smaller stromata, the outer layers of which became blackened. Two types of conidia were found in these locules. The first to be formed were of the beta type (Pl. XXXIV, Fig. 6) and were long-cylindric, straight or slightly curved, 1-celled, hyaline and 16–27 × 1–1.5 μ. These conidia were followed by and often intermixed with the alpha type of conidium (Pl. XXXIV, Fig. 5) which were fusoid-elliptic, 1-celled, hyaline and 7–12 × 2–3.5 μ.

In order to determine the effect of the host on the morphology of this fungus, this species was inoculated, on September 10, 1927, on steam-sterilized twigs of the following species of Acer: *A. saccharum* Marsh., *A. spicatum* Lam., *A. pseudoplatanus* L. and *A. platanoides* L. The general stromatic configuration was similar on all these species of Acer. Numerous, pustulate, erumpent-superficial, pycnidial stromata (Pl. XXXIV, Fig. 4.), 0.5–2 mm. in diameter, were formed and exuded spore masses or threads of a yellowish to olive color, containing both types of conidia as described above. Although these conidia varied within a fairly wide range of measurements, yet, as shown in Table I, this range of variation was practically the same for each host; the host or substratum showed no definite effect upon the size of the conidia. The pycnidia (Pl. XXXIV, Fig. 4) were composed partially of ectostromatic tissue formed on the bark surface and partially of entostromatic tissue within the surface bark layers. The conidial locules were spherical to ovoid or irregular and partially sunken in the bark tissue. There was a somewhat darkened zone of fungous pseudoparenchyma about the locules which were lined within by a hymenial layer of filiform conidiophores. Definite blackened marginal zones were formed about the entostromatic areas, which were occasionally limited in size (3–8 mm.), but were usually widely effuse and practically always possessed a sharp ventral zone. Mature perithecia were formed in two cultures on *A. saccharum* and perithecial initials appeared on one twig of *A. spicatum.* The asci in these perithecia measured 70–78 × 7–9 μ and the ascospores 11–12.5 (13) × 4–5 μ.

TABLE I

The Range of Variation in Size of the Alpha and Beta Conidia of *D. acerina* Pk.) Sacc., *D. dubia* Nit. and *D. celastrina* Ell. & Barth. from Cultures on Various Media and Hosts

Host or substratum	D. acerina		D. dubia		D. celastrina	
	alpha	beta	alpha	beta	alpha	beta
Oatmeal agar.........	7–12 × 2.5–3.5	16–27 × 1–1.5	8–11.5 × 2.5–4	9–11 × 1.3–2	6.5–10.5 × 2–3	16–23 × 1.3–1.5
A. spicatum..........	8–15 × 2.5–4	17–25 × 1–1.5				
A. saccharum.........	9–12 (13.5) × 2–3.5	17–25 × 1–1.5	9.5–14 × 2.5–4	10–12 × 1.3–1.5		
A. pseudoplatanus.....	9.5–13 × 2–3	19–25 × 1–1.5	9.5–12 × 2.5–3.5	8–12 × 1.3–1.5	6–9.5 × 2–3	16–23 × 1–1.3
A. platanoides........	9.5–12 × 2–3	(15) 19–27 × 1–1.5	9.5–12 × 2.5–4	8–12 × 1.3–1.5	5.5–8 × 2–3	14–20 × 1.3
A. rubrum............			9.5–14 × 2.5–4	9.5–12 × 1.3		
Berberis vulgaris......					5.5–8 × 2–2.5	16–24 × 1–1.3

DIAPORTHE DUBIA Nit.

Material of *Diaporthe dubia* Nit. collected on *Acer saccharum* Marsh. at Randolph, New Hampshire, is typical of the American form on *Acer saccharum*, which appears to be the same as Nitschke's type (Nitschke Herb. No. 61, Tilsinkiller, from Beckhaus) on *Acer negundo* L., *Diaporthe subcongrua* E. & E. (4, p. 425), *D. congener* E. & E. (4, p. 426), *D. ontariensis* E. & E. (4, p. 437) and *D. robusta* Pk. (14, p. 16) are all this same species. *D. congener* and some of the other synonyms have been reported on Fraxinus, but, as the dead twigs of Acer and Fraxinus might easily be confused, these reports need careful checking. This species differs from *D. acerina* in the more limited area of the entostromata, the incomplete ventral zone and the somewhat broader asci and ascospores.

The twigs from Randolph were placed in a damp chamber for three days and single-spore isolations made on July 27, 1927. The spores, which germinated within twenty-four hours, measured 15–16 × 5–6 μ and produced one or two germ tubes 2–3 μ in diameter.

On oatmeal agar this species produced a few pycnidial stromata very similar to those described for *D. acerina*, but smaller (0.3–2 mm.) and more scattered. Two types of conidia were found in these pycnidia. The alpha conidia (Pl. XXXIV, Fig. 10) were elliptic-fusoid, 1-celled, hyaline, 8–11 × 2.5–4 μ and very similar to those of *D. acerina*. The beta conidia (Pl. XXXIV, Fig. 11) were short-cylindric, usually curved but sometimes straight, allantoid, 1-celled, hyaline, 9–11 × 1.3–2 μ and quite distinct from those of *D. acerina*.

On August 12, 1927, this species was also inoculated on steam-sterilized twigs of *Acer saccharum*, *A. rubrum* L., *A. pennsylvanicum* L., *A. pseudoplatanus* and *A. platanoides*. Here again the stromatic structure was quite similar on all the hosts used as culture media. The pycnidial stromata (Pl. XXXIV, Fig. 12) were smaller (0.1–0.5 mm.) and much less strongly erumpent than, but otherwise very similar to, those of *D. acerina*. Both types of conidia were exuded in whitish to yellowish spore horns. In this species also, as shown in Table I, the range of conidial measurements was practically the same on all the hosts upon which it was cultured.

In *D. dubia*, the entostromata formed in culture were quite restricted in area, being 1–5 mm. in diameter. The ventral marginal zone was present, incomplete or entirely absent, but usually incomplete. On *A. pseudoplatanus* the wood tissues were blackened throughout and the entostromatic areas were somewhat more irregular than on the other hosts. No mature perithecia were found in these cultures. In general this species shows a less vigorous growth than *D. acerina* under the saprophytic conditions of growth in culture.

From these data it can be concluded that *D. acerina* (Pk.) Sacc. and *D. dubia* Nit. are two distinct species, limited in the former case to *A. spicatum* Lam. and in the latter to *A. saccharum* Marsh and perhaps also *A. negundo* L. and *A. saccharinum* L. Unfortunately, perithecial stromata are produced so seldom in culture that ascus, ascospore and perithecial characters could not be compared with any exactness. Sufficient other constant differences presented themselves, however, to separate the two species. *D. acerina* produced constantly, on all species of Acer, long cylindric, slightly curved, beta conidia (Pl. XXXIV, Fig. 6) measuring 16–27 × 1–1.5 μ, while *D. dubia* produced with equal consistency a short cylindric, allantoid type of beta conidium (Pl. XXXIV, Fig. 11) measuring 8–12 × 1.3–2 μ. The entostromata of *D. acerina* were nearly always widely effuse with a definite ventral zone, while those of *D. dubia* were limited in area on all the host species of Acer, with the ventral zone either present or absent. Although both these species can be cultivated saprophytically on a wide range of hosts, they appear to be quite limited as to their host species in nature. This can probably be explained by the fact that they infect the natural host as weak parasites, under which condition they are limited in some way as to their host.

DIAPORTHE CELASTRINA Ell. & Barth.

This species, occurring on *Celastrus scandens* L., is very similar to *D. acerina*, differing only in the somewhat smaller ascospores, 11–14 × 3–4 μ (Pl. XXXV, Fig. 3), and asci, 47–60 × 7–10 μ (Pl. XXXV, Fig. 2).

Single ascospores of *Diaporthe celastrina* Ell. & Barth. were isolated, on October 18, 1926, from material collected at Ithaca, New York, which was identical with type material (Ellis Herb. Myc. 183. 16 [2856], Clyde, Kans., 1901, from Bartholomew) in the Farlow Herbarium.

After being in a damp chamber for two days the ascospores of this material germinated profusely within twenty-four hours by means of a single germ tube 2.5–3 μ in diameter.

On oatmeal agar, numerous, erumpent, hemispherical to confluent stromata, 0.5–2 mm. in diameter, were formed. The locules in these pycnidia were comparatively large and spherical to irregular in shape. The outer, and particularly the upper, tissues of the stroma became brown with age. At first only one type of conidium was produced on agar cultures. This was the alpha type (Plate XXXV, Fig. 6), which was elliptic-fusoid, 1-celled, hyaline and measured 6.5–9.5 × 2.5–3 μ. Later the second or beta type (Pl. XXXV, Fig. 5) was found sparingly. These were long-cylindric, sharply hamate at one end, 1-celled, hyaline and measured 16–23 × 1.3–1.5 μ. The alpha conidia were usually found in orange-colored masses, while the beta conidia were always in whitish spore horns.

In order to test the effect of the host on its differential characters, this species was also inoculated on steam-sterilized twigs of *A. spicatum*, *A. pseudoplatanus*, *A. platanoides* and *Berberis vulgaris* L. On *Acer platanoides* and *A. pseudoplatanus* numerous erumpent-superficial stromata, many of which remained sterile, were formed, while on Berberis the pycnidial stromata were much smaller and not at all erumpent. On *A. plantanoides* there were no entostromatic areas produced and there was a very slight blackening of the tissues, while on *A. pseudoplatanus* numerous widely effuse entostromatic areas were produced and the wood tissues were more or less blackened throughout, as was the case with *D. dubia* on this host. On Berberis the few entostromata formed were limited in area (1–5 mm.), but possessed a definite ventral zone. No perithecial stromata were formed on any of these twigs, however, and these variations may have resulted from favorable or unfavorable growth conditions caused by either the substratum itself or the environmental conditions in the culture tubes. It does show, however, that such variations can take place within a single species and must be considered. The locules in the pycnidial stromata (Pl. XXXV, Fig. 4) were of varied shapes and often surrounded by a wall-like zone of blackened hyphae. Both types of conidia were found in these pycnidia and despite the stromatic variation on different hosts these conidia, as seen in Table I, showed no appreciable difference in their range of variation. The alpha conidia do, however, reveal a definitely lower range (5.5–8 (9.5) × 2–3 μ) in size than do those of *D. acerina* (8–13 (15) × 2–4 μ), corresponding to the smaller size of the asci and ascospores in *D. celastrina*. The range of variation in spore size and shape, therefore, appears to be a more constant character than stromatic configuration. *D. celastrina* appears to be a valid species limited to *C. scandens* as a host.

DIAPORTHE WOOLWORTHI (Pk.) Sacc.

The species here considered as *Diaporthe Woolworthi* (Pk.) Sacc. (15, 1 : 615) is either a synonym or perhaps a variety of *Diaporthe eres* Nit. (11, p. 245), the type species of the genus. *D. eres* represents an exceedingly large group of species which have been described on a large number of hosts and may in the future prove to contain a number of distinct host forms or varieties, but which at present it is impossible to separate on a morphological basis. This general group of species may be roughly described as follows: Appearing on the surface as numerous pustules or ruptures through which the short cylindric or slightly elongate ostioles are erumpent separately or in small clusters. Entostromata more or less widely and evenly effuse. Dorsal blackened zone present or absent. Ventral zone present or absent. Perithecia irregularly scattered or loosely clustered. Asci 40–60 × 5–8 μ. Spores 9.5–15 × 2.5–4 μ.

The American species on Ulmus (*D. Woolworthi*) differs from the European *D. eres* on the same host in the general lack of any blackened ventral zone in the wood. This American species was first described by Peck (12, p. 73) as *Valsa Woolworthi*. *Diaporthe ulmicola* E. & E. (5, p. 141) is this same species. Material which was collected on *Ulmus americana* L. at Ann Arbor, Michigan (Pl. XXXV, Fig. 7), and used as a source of cultures, was identical with Peck's type (N. Y. St. Mus., Greenbush, Sept., 1874) of *V. Woolworthi.* Ascospores (Pl. XXXV, Fig. 9) from this material germinated within twenty-four hours by a slight swelling of the spores, which were 12–13 × 4–5 μ, and by the production of two germ tubes, 3.5 μ in diameter, from each spore.

Single ascospore cultures of October 16, 1925, on oatmeal agar, produced a superficial mat of mycelium which, by December 7, had become compacted at various points to form irregularly spherical to pulvinate clusters of stromata, 1–2.5 mm. in diameter. One or several spherical to irregular locules were formed in these stromata. These pycnidial locules were lined with filiform hyaline conidiophores and sometimes were bounded by a zone of dark-walled fungous hyphae. Two types of conidia were formed. The alpha conidia (Pl. XXXV, Fig.11) were fusoid-elliptic, 1-celled, hyaline, measured 6–8.5 × 2–2.5 μ and occurred in yellowish-brown spore horns. The beta conidia (Pl. XXXV, Fig. 12) were long-cylindric, hamate, 1-celled, hyaline, measured 15–18 × 1 μ and were found in whitish spore horns.

This species was also cultivated on steam-sterilized twigs of various hosts. The following table shows the range of variation of the two types of conidia on these hosts:

HOST	ALPHA CONIDIA	BETA CONIDIA
Acer saccharum..........	5–8 (9) × 2–2.5 μ	11–19 × 1–1.5 μ
Corylus americana........	5.5–8 × 2–2.5 μ	11–19 × 1–1.3 μ
Ulmus americana.........	5–8 × 2–2.5 μ	13–19 × 1–1.3 μ
Spiraea sp................	5–9 × 2–2.5 μ	12 × 1 μ (very few seen)
Viburnum sp.............	5.5–8 × 2–2.5 μ	12–19 × 1 μ

From this it can be seen that the range of variation in size of the conidia is quite constant and practically the same for all the hosts used.

The pycnidia formed on stems (Pl. XXXV, Fig. 10) were similar to those in agar cultures, forming erumpent-superficial stromatic masses. On all the hosts except Acer and Ulmus the growth was quite restricted and very few pycnidial stromata were formed.

Entostromata were formed only on Ulmus. In culture these were often somewhat pustulate-effuse, with irregularly crowded or clustered perithecia and clustered, somewhat elongated ostioles. Such stromata and ostioles are typical of those found in *Diaporthe crinigera* E. & E. (3, p. 234) which may prove to be only a growth form of *D. Woolworthi.* This again shows that the stromatic configuration may vary under different growth conditions over a range including several species.

The relationships between this species and the numerous other described species of the *D. eres* group is too lengthy to be considered here. Imperfect stages have been assigned to many of the species of this group, but mostly by association only. Cultural data are limited to a few species. It will probably be possible to separate certain host species or varieties of this group when sufficient life-histories are known and it is with this end in view that these data are given as a basis for further comparison.

DIAPORTHE BECKHAUSII Nit.

This species on Viburnum is very similar to *Diaporthe eres* Nit., but differs in the fact that the entostromata are usually (but not always) limited in area (2–10 mm.) and in the fact that the dorsal zone often tends to dip into the bark to the wood surface, producing irregularly pustulate-effuse entostromata (Pl. XXXV, Fig. 13). *Diaporthe circumscripta* Fck. (Fung. Rhen. 1991), *D. anceps* (Sacc.) Petr. (Fl. Boh. & Mor. 1111) and *D. brachyceras* forma *viburni* Rehm (Rehm Asc. 2070) are also this same species. Material of *Diaporthe Beckhausii* Nit. collected on *Viburnum sp.* near Canton, Massachusetts, in December, 1925, was identical with type material in Nitschke's herbarium (No. 41, May, 1861).

Ascospores from the Canton material germinated sparingly and only after two or three days on Leonian's nutrient agar. Two long tortuously twisted germ tubes, 2.5 μ in diameter, were formed by each germinating spore.

On oatmeal agar numerous, superficial, hemispherical, whitish stromata, containing the usual spherical to irregular locules, were formed. Only one type of conidium was found in the yellow spore horns appearing in agar cultures. These were the alpha conidia

(Pl. XXXVI, Fig. 2), which were elliptic-fusoid, 1-celled, hyaline, and measured 8–11 × 2.5–3 μ.

This species was inoculated on steam-sterilized twigs of *Acer saccharinum* L., *Corylus americana* Walt., *Viburnum sp.* and *Spiraea sp.* on May 24, 1927. On all these twigs, numerous minute pustules, 0.1–0.4 mm. in diameter, were formed, caused by the production of small pulvinate ectostromata on the bark surface. These pycnidial stromata (Pl. XXXVI, Fig. 1) usually contained a single large, spherical locule which in age was bounded by a wall-like zone of dark-walled cells. Both types of conidia were formed on the twig cultures of all these hosts. The alpha type was similar to those formed on agar. The beta conidia (Pl. XXXVI, Fig. 3) were rather short cylindric, curved or crescent-shaped, 1-celled, hyaline, and measured 8–13 × 1–1.5 μ. These beta conidia were often sparingly produced and occurred in white spore horns. The following table shows the range of size of the two types of conidia on the various hosts:

HOST	ALPHA CONIDIA	BETA CONIDIA
Acer saccharinum...........	9–12 × 2–3 μ	9–12 × 1.3–1.5 μ
Corylus americana..........	8.5–11 × 2.5–3 μ	9.5–12(13) × 1–1.5 μ
Viburnum sp...............	9–12 × 2–3 μ	8–13 × 1–1.5 μ
Spiraea sp.................	9–12 × 2–3 μ	9.5–13 × 1.5 μ

Here again the host made very little or no difference in the range of conidial size or shape. Entostromata were abundantly formed on Viburnum and Spiraea and to a lesser degree on Ulmus and Corylus. Wherever they were formed, they usually possessed a definite ventral zone and were definitely limited in area (1–15 mm.), so that in this species these differential stromatic characters appear to be good ones correlated with the shorter crescent-shaped beta conidia.

Nitschke (11, p. 245) gives the "stylospores" of *D. Beckhausii* as filiform, curved and 10–12 × 1 μ. Cooke (2, p. 91) describes a *Phoma Beckhausii*, with "sporules" sublanceolate, continuous and 8–10 × 3 μ, as associated with *D. Beckhausii*. Traverso (16, p. 269) later gives this as *Phomopsis Beckhausii* (Cke.) Trav. and as the imperfect stage of *D. Beckhausii*. Von Höhnel (9, p. 681) states that *Phoma tinea* Sacc. (Mich., I : 521), with conidia fusoid and 8 × 2 μ, is the imperfect stage of *D. Beckhausii*. The measurements of the conidia given by these various writers agree very well with the two types of conidia obtained in cultures of this species.

DIAPORTHE VIBURNI Dear. & Bisby var. **spiraeicola**, var. nov.

This variety, collected by the writer on *Spiraea tomentosa* L. near Arlington, Massachusetts, in May, 1927, may be briefly described as follows: Appearing on the surface as numerous minute pustules or ruptures of the periderm. Ostioles short, conical, erumpent separately or in small loose groups. Perithecia (Pl. XXXVI, Fig. 4) spherical, 320–480 μ in diameter, loosely scattered or crowded, in the bark or wood. Neither a dorsal nor a ventral zone present, but sometimes a slight blackening above the individual perithecia. Asci (Pl. XXXVI, Fig. 5) clavate with a refractive ring in the apex and measuring 58–65 × 7–10 μ. Ascospores (Pl. XXXVI, Fig. 6) biseriate, 14–17.5 × 5.5 μ.

At the time of collection this Diaporthe was considered a new species, but material of *Diaporthe viburni* Dear. & Bisby (description now in press) on *Viburnum lentago* L. kindly sent to the writer by Dr. Dearness proved to be so similar that the two were thought to be identical. *D. viburni* differs from *D. evonymi* Dear. chiefly in the absence of any ventral zone. Inasmuch as the variety on Spiraea has somewhat larger perithecia more deeply seated in the bark or wood and has formed ventral zones in culture, its identity with *D. viburni* is doubtful and it is here provisionally presented as a variety of that species.

On May 21, 1927, sprays of ascospores from the material collected on Spiraea were made on Leonian's agar. After two days no germination occurred. After five days colonies appeared, but no germination had been observed. Twigs were then placed in a damp chamber for four days and sprays again made on May 30. Only a few cases of delayed germination were seen after six days. Twigs were again placed in a damp chamber for four days and sprays made on June 6. These spores germinated abundantly within twenty-four hours. As often happens on Spiraea, large numbers of pycnidia were formed on the stems, but perithecia were rather sparsely produced, and the ascospores were probably immature. The germinating spores measured 16–17 × 5–5.5 μ and produced one or, rarely, two germ tubes 3–4 μ in diameter.

Single-spore cultures on oatmeal agar produced, within two weeks, numerous, small (0.5–1 mm.), hemispherical or pulvinate, pycnidial stromata which exuded yellowish to orange masses of conidia. The pycnidia contained irregular, usually flattened locules which were bounded by a zone of dark-walled hyphae. Conidia of the alpha type (Pl. XXXVI, Fig. 8) only were found in these cultures. These conidia were elliptic-fusoid, 1-celled, hyaline, and measured (8) 9–13 × 2.5–3 μ.

Inoculations of this species were made on steam sterilized twigs of *Acer saccharinum*, *Ulmus americana*, *Corylus americana*, *Viburnum sp.* and *Spiraea sp.* On all these hosts numerous, often crowded, minute ectostromata, 0.1–0.3 mm. in diameter, were formed on the bark surface and were erumpent through the periderm. Most of these stromata remained sterile, but in some of them small irregular or flattened locules (Pl. XXXVI, Fig. 7) were formed. Both types of conidia were formed in these pycnidia on stems. The beta conidia (Pl. XXXVI, Fig. 9) were long filiform, strongly curved or hamate, 1-celled, hyaline, and measured (15) 20–33 × 1 μ. They were found in white spore horns. The range in size of the conidia on the various hosts is shown below.

HOST	ALPHA CONIDIA	BETA CONIDIA
Acer saccharinum....	8–11 (13) × 2.5–3 (4) μ	none seen
Ulmus americana....	8–11 (13) × 2.5–4 (5) μ	20–33 × 1 μ
Corylus americana...	8–12 × 2–3 μ	16–33 × 1 μ
Spiraea sp...........	8–12 (15) × 2.5–3 μ	19–29 × 1 μ
Viburnum sp........	8–15 × 2.5–3.5 μ	15–33 × 1 μ

From these data it can be seen that, although the range in variation in size appears to be greater on some hosts than on others, yet there are no definite host differences; these variations are probably caused by the conditions of the culture tubes rather than by the host. On all the hosts except Viburnum definite entostromata were formed and were usually somewhat limited in area. On Acer and Corylus the blackened zones formed in culture were usually only lateral, but on Spiraea and Ulmus definite ventral zones were also produced. Mature perithecia were found on both Acer and Spiraea. The asci on both these hosts were 65–75 × 9–12 μ and the ascospores 13.5–16.5 × 4.5–5.5 μ.

The occurrence of definite lateral and ventral zones on the stems in culture is a distinct departure from the configuration found under natural conditions and may indicate that this variety is more closely related to *D. evonymi*, from which it was supposed to differ in just this character. This question can be determined only by a study of Spiraea material and a cultural comparison with *D. evonymi* and *D. viburni.*

DIAPORTHE TUBERCULOSA (Ell.) Sacc.

Material of *Diaporthe tuberculosa* (Ell.) Sacc. was collected on *Amelanchier canadensis* (L.) Medic. at Ithaca, New York. It appears on the surface as perforations of the periderm, through which the loosely clustered cylindrical ostioles are erumpent. The entostromata are isolate to pustulate-effuse (Pl. XXXVI, Fig. 10), limited in area (2–10 mm.), lighter in color than the rest of the bark, and possess a definite ventral zone. The dorsal zone usually ends abruptly at the bark surface and does not continue along this surface, as often happens in other species. The perithecia are loosely clustered, often in definite pustulate areas of the entostroma. The asci (Pl. XXXVI, Fig. 12) are 70–80 × 11–13 μ. The spores (Pl. XXXVI, Fig. 11) are biseriate, broad elliptic-fusoid, constricted at the septum and 12–14 × 4.5–5.5 μ.

Peck's variety *dissepta* (13, p. 28) of *D. tuberculosa,* given as having larger perithecia (500–625) and separately erumpent ostioles, comes within the range of variation of the species. The variety *pruni* Dear. & House (10, p. 31) on Prunus appears quite distinct, having a sharp raised ridge on the surface of the twig outlining the entostromatic areas, and also somewhat smaller spores (10–13 × 4–5 μ). As will be shown later, however, this may be considered as merely a growth form of *D. tuberculosa.*

Ascospores of the material mentioned above were sprayed on agar on September 13, 1926. These spores germinated within twenty-four hours by means of a single germ tube 4–4.5 μ in diameter.

Single-spore cultures on oatmeal agar produced numerous, grayish, pulvinate to confluent, pycnidial stromata in the following manner. A stromatic, irregularly thickened layer of compacted hyaline hyphae which took a deep stain with eosin was formed on the surface of the agar, representing the ectostromata formed on the bark surface of twigs. A similar proliferation of hyaline but deeply staining hyphae also took place within the surface layers of the agar. A superficial crust of blackened, thick-walled pseudoparenchyma cells was formed upon the irregular surface of these stromatic areas. This dorsal blackened zone then penetrated into the agar and continued along the ventral margin of the immersed stromatic areas as a compacted pseudo-parenchymatous, somewhat blackened margin, simulating the ectostromatic and entostromatic development on twigs. The irregularly shaped, often flattened pycnidial locules arose in the superficial or ectostromatic portion of these stromata. The conidia first produced were of the beta type (Pl. XXXVI, Fig. 15) and were long cylindric-fusoid, curved, tapered at the ends, crescent-shaped, 1-celled, hyaline, and measured 11–20 × 1.3–1.5 (2) μ. The alpha conidia (Pl. XXXVI, Fig. 14), which were formed later, were elliptic-fusoid, 1-celled, hyaline, and measured 7–12 × 3.5–4.5 (5) μ.

On September 19, sterilized twigs of *Amelanchier canadensis* (L.) Medic. and *Acer pennsylvanicum* L. were inoculated from single-spore cultures of this species. Erumpent-superficial ectostromata appeared upon these twigs after three to four weeks. These ectostromata usually occurred on the surface of the entostromatic areas of the bark which were somewhat limited in area and definitely outlined beneath by a ventral blackened zone. The flattened pycnidial locules (Pl. XXXVI, Fig. 13) usually occurred in the entostromatic areas of the bark. Both types of conidia were formed. The alpha conidia were 9–12 × 3.5–4.5 μ, and the beta conidia were 11–18 × 1–1.5 (2) μ. In several of the cultures on Amelanchier twigs, the line where the marginal zone of the entostromata abutted upon the periderm appeared on the surface as a sharp ridge outlining the entostromatic areas. This appears as a quite striking difference in structure and has been described by House (10, p. 31) as variety *pruni* Dear. & House on *Prunus serotina.* The type (Fl. N. Y., Glenwood, Oneida Co., May, 1915) of this variety has somewhat smaller spores (10–13 × 4–5 μ) than *D. tuberculosa,* but since this may be due to immaturity, it seems probable that it is merely a growth form of that species. The ventral zones were usually not so strongly developed on the twigs of *Acer pennsylvanicum,* but here also the superficial outlining ridges often appeared.

The *Phoma amelanchieris* of Cooke (2, p. 93) with subfusiform conidia, 8 × 2.5–3 μ, on sporophores three times as long, may be the same as the conidial stage obtained in culture.

CONCLUSIONS

The foregoing results show that, as in most situations of this sort, generalities are dangerous and that determinations of the range of variation or constancy of characters should be made rather individually for each species or group of related species. Unfortunately perithecial formation is so erratic under cultural conditions that nothing definite could be determined concerning ascospore or perithecial characters. The data on stromatic characters and imperfect stage connections, however, do bring out certain points. In the first place, stromatic characters are likely to be more plastic and variable than conidial characters. As indicated under *D. Woolworthi* and *D. tuberculosa,* quite striking variations in stromatic configuration, often of varietal or specific rank, may take place under varying growth conditions. On the other hand, certain definite tendencies or differences in range of variation of stromatic characters may be quite constant and characteristic, and when correlated with the host, as in *D. acerina* and *D. dubia,* or *D. Beckhausii,* may indicate definitely separated species. Secondly, conidial size and shape appear to be quite constant, within a given range of variation for each species, on a large variety of hosts or substrata, as was true of all the species cultured. That is, no definite difference in range of size and shape of conidia was correlated with any particular host in any one species. Thirdly, specific separations on slight morphological differences in the perithecial stage often become more pronounced when the imperfect stage is known because of the occurrence of correlated differences in this stage of the life-history, as in *D. acerina* and *D. dubia.* Fourthly, morphological differences in both the perithecial and conidial stages are often definitely correlated with the host, indicating that closely related species with slight morphological differences are often definitely limited as to their host species under natural conditions. These same species, again, may be cultivated on a number of hosts saprophytically in the laboratory. The exact explanation for such a limitation in nature is as yet undetermined, but is probably linked up with the fact that many of these forms begin their existence in nature as weak parasites, and in this condition are limited in their host range. It is quite probable, therefore, that many host species or varieties may be separated in the future from the more complex "species groups" of this genus.

SUMMARY

1. Cultural connection of the conidial stage of *D. acerina* (Pk.) Sacc., *D. dubia* Nit., *D. celastrina* Ell. & Barth., *D. Woolworthi* (Pk.) Sacc., *D. Beckhausii* Nit., *D. viburni* Dear. & Bisby var. *spiraeicola,* var. nov., and *D. tuberculosa* (Ell.) Sacc. were obtained in single-spore cultures.
2. All these species produced pycnidia of the Phomopsis type with both alpha and beta conidia.
3. These species were cultivated saprophytically on various host twigs in order to determine the effect of the host upon the variation of morphological characters.
4. Stromatic characters were found to be quite variable in some species and more or less constant in others. The range in variation of size and shape of the conidia was constant on the various hosts and often typical of the species.
5. Morphological differences in both the perithecial and conidial stage were often found correlated with a host genus or species indicating fungous species narrowly limited as to host.
6. *Diaporthe viburni* Dear. & Bisby var. *spiraeicola* is described as a new variety.

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EXPLANATION OF PLATES XXXIV–XXXVI

PLATE XXXIV

Diaporthe acerina (Pk.) Sacc.

FIG. 1. Vertical section of perithecial stroma, showing widely pustulate-effuse entostromata with definite vertical zone

FIG. 2. Ascospores

FIG. 3. Ascus with ascospores

FIG. 4. Vertical section of pycnidium as formed in culture on twigs

FIG. 5. Alpha conidia produced in culture

FIG. 6. Beta conidia produced in culture

Diaporthe dubia Nit.

FIG. 7. Vertical section of perithecial stromata, showing entostromata limited in area and with an indefinite ventral zone

FIG. 8. Ascospores

FIG. 9. Ascus with ascospores

FIG. 10. Alpha conidia produced in culture

FIG. 11. Beta conidia produced in culture

FIG. 12. Vertical section of pycnidium as formed in cultures on twigs

PLATE XXXV

Diaporthe celastrina Ell. & Barth.

FIG. 1. Vertical section of perithecial stromata, showing type of entostroma

FIG. 2. Ascus with ascospores

FIG. 3. Ascospores

FIG. 4. Vertical section of pycnidium as formed in culture on twigs

FIG. 5. Beta conidia produced in culture

FIG. 6. Alpha conidia produced in culture

Diaporthe Woolworthi (Pk.) Sacc.

FIG. 7. Vertical section of perithecial stroma, showing irregularly clustered perithecia, evenly effused dorsal zone and lack of ventral zone

FIG. 8. Ascus with ascospores

FIG. 9. Ascospores

FIG. 10. Vertical section of pycnidium as formed in culture on twigs

FIG. 11. Alpha conidia produced in culture

FIG. 12. Beta conidia produced in culture

Diaporthe Beckhausii Nit.

FIG. 13. Vertical section of perithecial stromata, showing irregularly pustulate-effuse stromata, somewhat limited in area and with a definite ventral zone

FIG. 14. Ascus with ascospores

FIG. 15. Ascospores

PLATE XXXVI

Diaporthe Beckhausii Nit.

FIG. 1. Vertical section of pycnidium as formed in culture on twigs

FIG. 2. Alpha conidia produced in culture

FIG. 3. Beta conidia produced in culture

Diaporthe viburni Dear. & Bisby var. *spiraeicola*, var. nov.

FIG. 4. Vertical section of perithecial stroma, showing scattered perithecia with neither dorsal nor ventral zones

FIG. 5. Ascus with ascospores

FIG. 6. Ascospores

FIG. 7. Vertical section of pycnidia as formed in culture on twigs

FIG. 8. Alpha conidia produced in culture

FIG. 9. Beta conidia produced in culture

Diaporthe tuberculosa (Ell.) Sacc.

FIG. 10. Vertical section of perithecial stromata, showing entostromata somewhat limited in area and with a definite ventral zone

FIG. 11. Ascospores

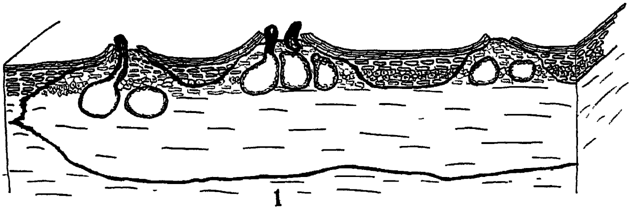
FIG. 12. Ascus with ascospores

FIG. 13. Vertical section of pycnidium as formed in culture on twigs

FIG. 14. Alpha conidia produced in culture

FIG. 15. Beta conidia produced in culture

PLATE XXXIV



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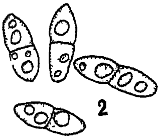

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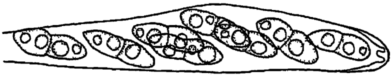

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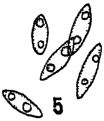

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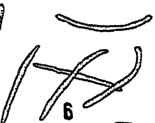

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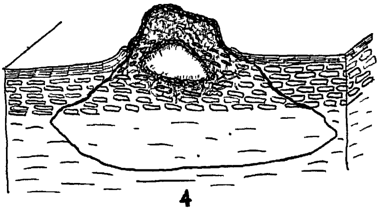

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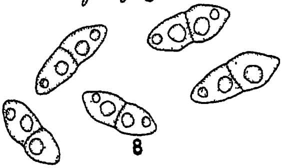

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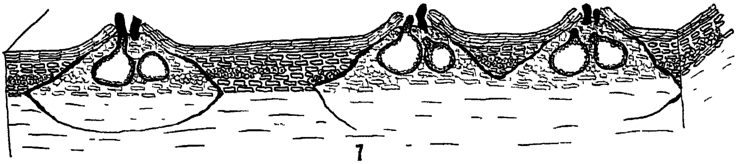

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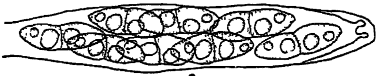

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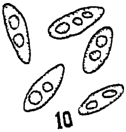

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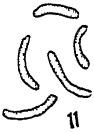

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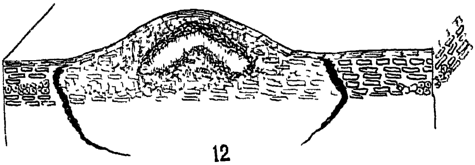

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PLATE XXXV

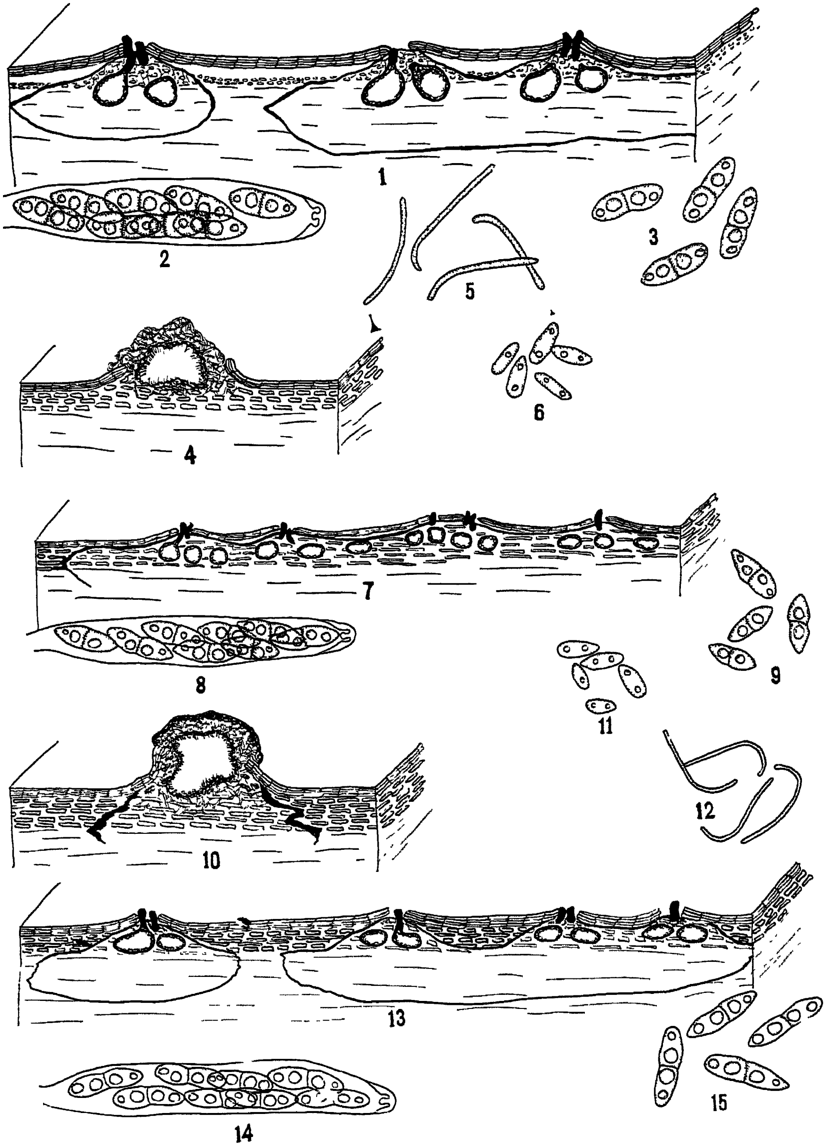
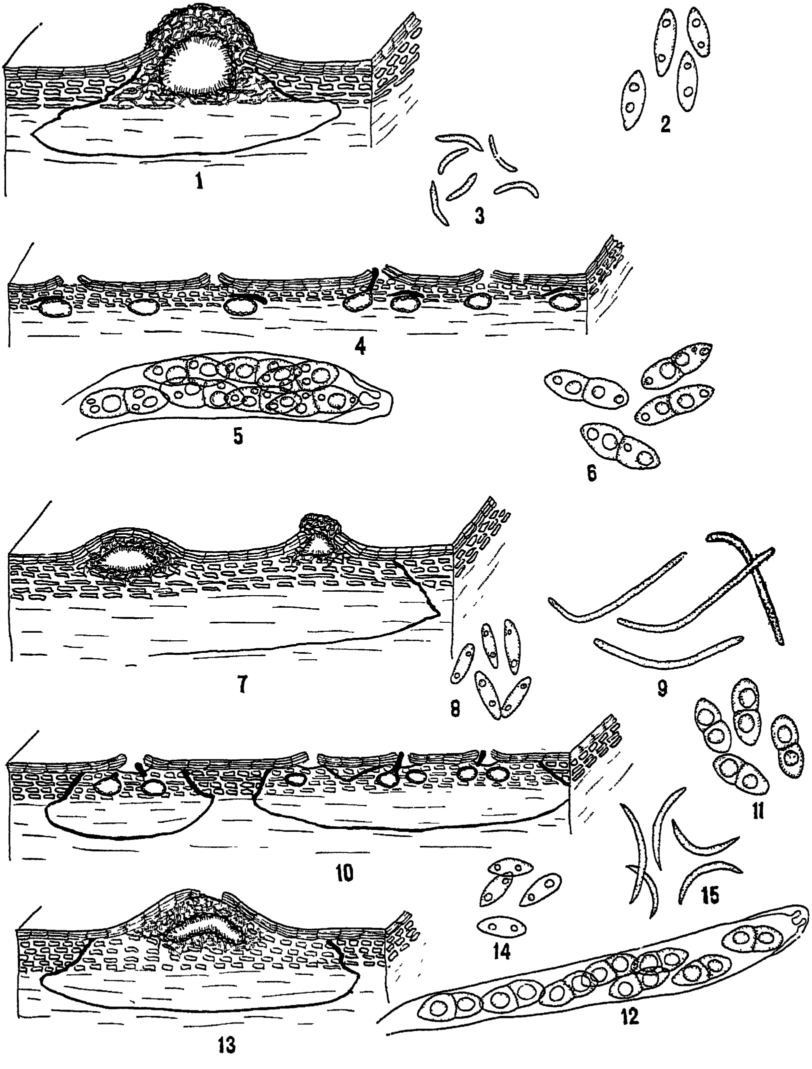


PLATE XXXVI



A NATURAL SECTORIAL CHIMERA OF THE SUNFLOWER (*HELIANTHUS DIVARICATUS* L.)

EDWARD F. WOODCOCK

THE investigation of chimeras has been largely with those resulting from grafting practices. H. Winkler (2) was the founder of the experimental study of the chimeras and published the result of his work in 1914. Other investigators have carried on somewhat similar studies and there is much information available in the literature concerning various chimeras as they are sometimes observed in nature.

There has arisen much difference of opinion regarding the interpretation of the striking chimeras obtained as a result of grafting, in which the plant consists of two components. One theory is that the new productions (such as the Solanum chimera reported by Winkler), which are not obvious chimeras, none the less resemble the latter in maintaining the individuality of the two components. The portions of each are aggregated into a sort of patchwork or mosaic. Another theory has resulted from a microscopic study by Baur (1) of the variegated geranium *Pelargonium zonale* Willd., whose leaves have a white margin. He found that one of the graft symbionts may act as a mantle for the other. In this case the body of the new form consists entirely of one variety, while the epidermis alone, or the epidermis with the hypodermis, is composed entirely of the other variety. These interesting forms have been termed periclinal chimeras. It is generally considered now that *Cytisus adami* Port. is a periclinal chimera, the body being composed of *Laburnum vulgare* Griseb. and the epidermis of *Cytisus purpuri* Scop. There is reason to believe that the Crataegomespilus chimeras are periclinal in structure, with the interior made up of Crataegus covered by a one- or two-layered skin of Mespilus.

In all these cases a seedling gives rise not to an intermediate form but to a form like one of the symbionts. Most of the supposed graft hybrids are in reality periclinal chimeras, since, in the last analysis, a graft hybrid should differ from all kinds of chimeras in the merging of the protoplasm of the two graft symbionts. Such a merging of the protoplasm has not yet been conclusively demonstrated.

This brief paper deals with a natural sectorial chimera of *Helianthus divaricatus* L. collected in July, 1928, by E. A. Watson at Lansing, Michigan. No internal anatomical studies were made of the plant as it was in a wilted condition when shown to the writer. A careful description and interpretation of the conditions evident in an external examination of the plant may be of interest to those who are carrying on investigations of chimeras.

The plant was in the flowering stage and consisted of six nodes bearing decussate leaves. The green tissue of the plant was included in a sector which represented one fourth of the plant body; the other three fourths lacked the chlorophyll more or less completely. The line of demarkation, on each side of the sector, between the two regions, was very clearly marked in the upper half of the plant body. One line passed along the midrib of a leaf while the other passed in such a way that an entire leaf was lacking in chlorophyll content. In the lower half of the plant the line of demarkation did not hold so strictly to the midrib of the leaf, but in every case at least one sixth of the leaf blade was lacking in chlorophyll. It is interesting to note that the affected tissue regions showed a greater lack of chlorophyll in the upper portion of the plant body than in the lower portion. In the latter location the regions showed a yellow-green mottling due to the fact that the chlorophyll was lacking only in islands of tissue scattered among the tissues bearing chlorophyll. In the upper part of the plant, a portion of which is shown in Plate XXXVII, Figure 1, these islands of tissue without chlorophyll have come to occupy almost completely the affected sector, nearly to the exclusion of the green tissue.

A study of Figures 1 and 2 will give an understanding of the probable sequence of events in that portion of the plant represented.

There is shown, at the left of the plant, a series of diagrammatic cross-sections (Fig. 2) in which that portion corresponding to the green tissue is shaded and the cross-sections are arranged so that the bottom of each corresponds to the front of the stem. At *B* it is seen that three fourths of the stem lacks chlorophyll, since all of the right leaf and one half of the left lack chlorophyll. It is obvious from the data given above that, as the central axis continues into the central inflorescence, the front bracteal leaf and the left half of the posterior bracteal leaf lack chlorophyll. All the tissues in the right inflorescence lack chlorophyll since they have originated from an axillary bud at *B* in that half of the stem in which all the cells lack chlorophyll. In the left inflorescence one half of the tissues lack chlorophyll since they have originated from an axillary bud at the node *B* located on the line between the green tissue and the tissue without chlorophyll.

Our knowledge of the heredity of white- and green-leaved chimeras rests largely on the work of Baur with the geranium. A probable explanation of the two-color phenomenon is the occurrence of a vegetative factor mutation in the meristematic tissue causing the development of a chimera. The Helianthus chimera is considered to be sectorial in nature since the lateral organs of such chimeras are produced from buds starting in green or white tissue or on the line between the green and white tissue, whereas periclinal chimeras are produced by an overgrowth of one colored tissue about the other.

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DESCRIPTION OF PLATE XXXVII

Sunflower chimera

FIG. 1. Terminal portion of Helianthus chimera, showing the distribution of the white and green tissue. The labels indicate the location of the various diagrammatic cross-sections shown in Figure 2.

FIG. 2. A series of diagrammatic cross-sections of the Helianthus chimera made at intervals along the plant axis. The shaded areas represent the green tissue and the bottom of each cross-section corresponds to the front of the plant shown in Figure 1.

PLATE XXXVII

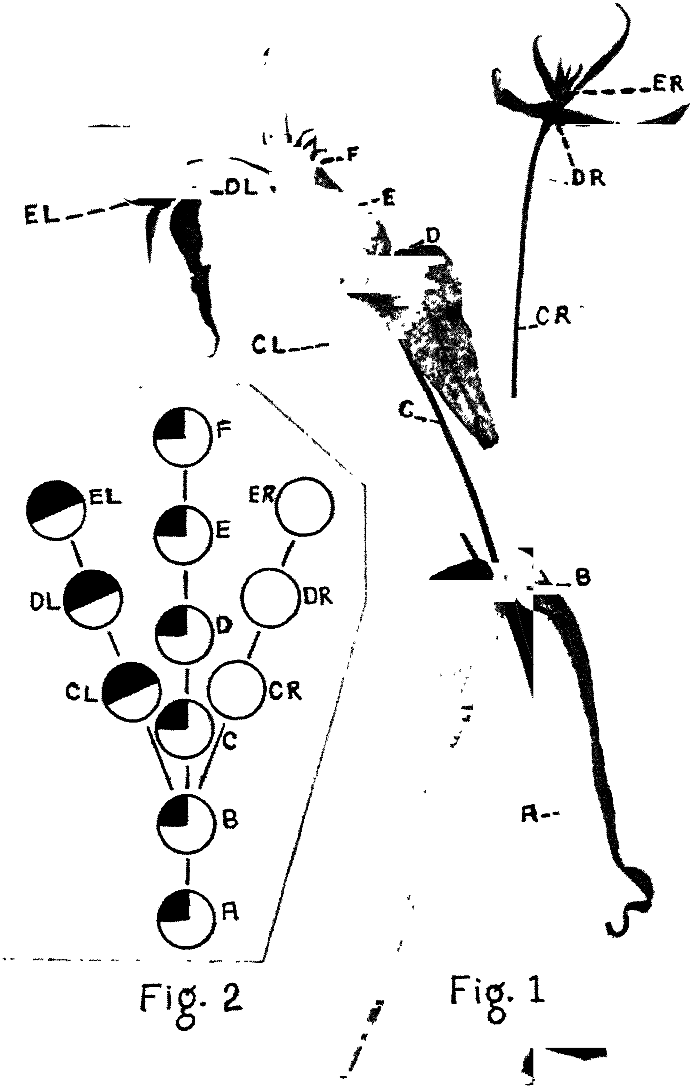

Fig. 2

Fig. 1

Sunflower chimera

ANATOMY OF THE LEAF OF THE BLACK RASPBERRY (*RUBUS OCCIDENTALIS* L.)

EDWARD F. WOODCOCK

INTRODUCTION

THE external leaf characters of the black raspberry have been mentioned by the various systematic botanists who have described the plant, but very little work has been done upon the internal anatomy of the leaf. Fritsch (1) published a very complete work in 1887 on anatomical-systematic studies of the Genus Rubus, in which he presented the results of a histological investigation of a series of species which are representative of the larger subgenera. In the subgenus Idaeobatus, to which the black raspberry belongs, he states that the leaf petiole shows in cross-section three vascular bundles, the median one larger than the two small lateral bundles. He figures a diagrammatic cross-section of the petiole of *Rubus idaeus* L. and a detailed drawing of a portion of the petiole of *Rubus squarrosus* Fritsch, but he includes no detailed study of the leaf of *Rubus occidentalis* L.

The writer has in progress a careful anatomical study of the various vegetative organs of the black raspberry, *Rubus occidentalis* L. The present paper reports his observations on the histology of the leaf.

MATERIAL AND METHODS

The material for study was obtained from potted black raspberry plants and from dried herbarium specimens. Microtome sections, stained with methyl green and Bismarck brown, were used for an interpretation of the tissues.

GROSS MORPHOLOGY

The alternate leaves are spirally arranged on the stem and the basal portion of the petiole is somewhat broadened at its point of attachment to the stem. The narrow bristle-like, deciduous stipules are adnate to the petiole for about half their length. The lamina of the leaf (Pl. XL, Fig. 9) is broad, rounded and pinnately divided into three leaflets each of which is ovate, acuminate, coarsely incised-serrate and very white-pubescent beneath. The lateral leaflets are short stalked. Occasional small, hooked prickles occur on the petiole, leaflet stalks (Fig. 8), and on the lower side of the main veins. The venation is of the netted type. The main lateral branches arise from a strongly developed midrib and run obliquely outward to the teeth. The smaller veins anastomose freely, with ultimate branches ending blindly in the parenchyma of the intercostal fields.

ANATOMY

As seen in cross-section, the three leaf traces of the petiole (Text Fig. 7) form a crescent open toward the ventral side of the petiole. The median bundle is larger and broader than the two lateral bundles and is also somewhat concave on its ventral side. The ontogeny of the vascular tissue of the stipules, petiole and lamina is discussed later in this paper.

The bundles of the stipules are narrow and consist of a few thin-walled phloem elements and two or three narrow, spiral xylem elements. The bundles of the petiole are surrounded on all sides by cortical tissue which merges into collenchyma just beneath the epidermis. The parenchyma tissue of the cortex is made up of a region of irregularly arranged, barrel-shaped cells which form a layer from six to eight cells in width. Intercellular spores are also evident in this region. The walls of the several-celled layer of elongated collenchyma are thickened in such a way that the tissue has a stratified appearance (Text Fig. 7 and Pl. XXXVIII, Fig. 6). The collenchyma is continuous about the periphery of the petiole except directly below the stomata, where it is replaced by parenchyma tissue. In radial longitudinal section the collenchyma cells appear several times longer than broad. Directly inside the collenchyma region are one or two layers of small, nearly isodiametric parenchyma cells in which chloroplasts are abundant (Pl. XXXIX, Fig. 12). Chloroplasts also occur, less abundantly, in the collenchyma and parenchyma adjacent to this tissue. The epidermal cells of the petiole are small, angular, irregularly arranged and nearly isodiametric. Numerous short one-celled hairs occur on the surface. The xylem portion of each petiole leaf trace is made up of radially arranged rows of spirally thickened tracheids, which increase in diameter from the protoxylem to the phloem. Between the rows of tracheids are elongated parenchyma cells (Pl. XXXVIII, Fig. 8). The xylem partially encircles the phloem at each side of the bundle. The cambium is poorly differentiated between the phloem and xylem. The phloem is made up of small, narrow sieve tubes which are from eight to ten times as long as broad and each tube has a large, slightly flattened nucleus imbedded in the abundant cytoplasm. The cross-walls are slightly thickened to form the sieve plates (Pl. XXXIX, Fig. 11). Among the groups of small sieve tubes occur occasional broader parenchyma cells. In contact with the sieve tissue of each trace there are present groups of bast fibers, which become very thick walled when the leaf is mature. This bast tissue forms a continuous cap over the phloem in the lateral traces.

FIG. 7. Cross-section of petiole (× 80)

The upper epidermis of each leaflet is slightly thicker than the lower epidermis and the cells are larger in tangential extent (Pl. XXXVIII, Figs. 3, 7, 10). The radial walls are less wavy in outline. The outer walls of both epidermises are slightly cutinized and no stomata appear in the upper epidermis. In the lower epidermis the numerous stomata are irregularly arranged. No definite counts were made of the number of stomata since the numerous, interlacing, sinuous hairs arising from the lower epidermis form such a compact mat that it is almost impossible to remove the epidermis intact. These hairs (Fig. 9) are thin-walled and usually somewhat appressed. The mat of hairs is often as thick as the lamina itself. Scattered, stiff, thick-walled hairs (Fig. 1) occur along the main veins, both on the dorsal and ventral side of the leaf.

The mesophyll (Fig. 10) includes two layers of palisade tissue and rather compact spongy tissue. The cells of the inner layer of palisade tissue are shorter and broader than the outer layer. Figure 11, an end view of the palisade cells, shows how loosely the cells are arranged. The shape of the spongy cells when seen through the lower epidermis is shown in Figure 4.

The midrib has one large central vascular bundle (Fig. 2), which gives rise to all the lateral veins except the first small veins at the base of the lamina. The latter are a continuation of the two small bundles of the leaflet stalk. The lateral veins are surrounded by a sheath of parenchyma cells in which only a few chloroplasts are present (Fig. 5). The vascular tissue becomes reduced to several spiral tracheids and sieve tubes with a few parenchyma cells. No fibrous tissue is evident. The vein ending is composed of one or two spiral tracheids surrounded by a parenchyma sheath.

ONTOGENY OF THE VASCULAR SUPPLY

The first indication of the development of the leaf traces from the procambium ring is seen in the pushing out of segments of the ring (Pl. XXXIX, Fig. 1). Of the three traces thus coming into existence, the two lateral traces separate from the ring before the median one (Fig. 2). At this stage the branch trace appears horseshoe-shaped in cross-section. The median leaf trace which forms the toe of the shoe separates from the branch trace before the branch gap is closed (Fig. 3). The closing of the branch gap is soon followed by the separation of the branch trace from the procambium ring of the stem axis (Fig. 4).

Each of the two lateral leaf traces soon begins to divide into three unequal parts, the largest part toward the median trace (Fig. 5). The smallest portion separates from the other two before the latter completely divides (Fig. 6). Very soon the division is complete and the base of the petiole has seven traces (Fig. 7). Each of the two small lateral traces passes out as a stipule trace. Of the two small traces remaining in each side of the petiole, one fuses with the median trace, thus forming a median three-lobed trace (Fig. 8) which soon loses its lobed appearance and becomes crescent-shaped (Fig. 9). In the stage shown in the latter figure, the stipules have separated from the petiole and each stipule has a single central trace.

The three petiolar traces keep a parallel position throughout the length of the petiole and anastomose as they enter the base of the ternately divided lamina. The first indication of a change in the behavior of the traces is the three-lobing of the median trace and the appearance of a small lobe on each of the two lateral traces (Pl. XL, Fig. 1). As the lobes become more pronounced in the median trace, the lobed lateral traces fuse with the median trace (Fig. 2), and the central lobe of the median trace becomes distinct (Fig. 3). Each lateral trace now has three lobes, the smallest lobe toward the ventral side of the petiole. This lobe soon separates from the other two lobes and the larger of the two latter moves toward the center of the petiole (Fig. 4) and becomes separated as a distinct trace (Fig. 5). The anastomosing region now has three large traces and four small traces. Finally two of the small traces, which are located next to the median trace, divide (Fig. 6) and the stalk of each leaflet thus has one large median trace and two small lateral traces (Fig. 7). A cross-section of the leaflet stalk shows a distinct furrow along the ventral side (Fig. 8). In the lateral traces the xylem of the bundle is toward the furrow. In Figure 8 there is also shown a large prickle in outline. The two lateral traces become the first veins at the base of the lamina of each pinnately veined leaflet and the median trace forms the midrib and sends off branches to form the lateral veins next beyond the first veins (Fig. 10).

SUMMARY

The stipules are narrow, partially adnate and deciduous. The petiolar vascular tissue is composed of a large median trace and two smaller lateral traces. The xylem tissue includes rows of radially arranged, spiral tracheids and parenchyma cells, and the phloem includes groups of small, narrow sieve tubes which have abundant cytoplasm and a large nucleus to each segment of the tube. Occasional phloem parenchyma cells occur separating the groups of sieve tubes. Cambium is poorly developed and the fibrous tissue adjacent to the sieve tissue becomes well developed as the leaf comes to maturity. The cortex of the petiole has short barrel-shaped parenchyma and elongated collenchyma cells. The lamina mesophyll has typical compact palisade and spongy tissue. Numerous, irregularly arranged stomata are present in the lower epidermis. The lower side of the leaf is covered with a mat of intertwined, long, thin-walled, sinuous hairs. An ontogenetic study of the vascular tissue shows that the three petiolar traces anastomose at the base of the leaflets and the stalk of each leaflet is furnished with the same trace arrangement as the petiole. The small lateral traces supply the first lateral veins and the median trace forms the midrib from which arise all other lateral veins.

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DESCRIPTION OF PLATES XXXVIII–XL

Leaf of *Rubus occidentalis* L.

Abbreviations used: L, lamina; X, xylem; P, phloem; UE, upper epidermis; BS, bundle sheath; LE, lower epidermis; BH, base of hair; IS, intercellular space; C, collenchyma; EP, epidermis; ST, stoma; GC, guard cell; CH, chloroplast; ST, spiral tracheid; XP, xylem parenchyma; CA, cambium; STU, sieve tube; BF, bast fiber; SP, spongy tissue; PA, palisade tissue; CO, cortex; PR, prickle; LT, leaf trace; BT, branch trace; PR, procambium ring; SE, stipule; SR, stipule trace.

PLATE XXXVIII

FIG. 1. Thick-walled, stiff hairs from over a vein (× 166)

FIG. 2. Diagram of cross-section of leaf through midrib. Limit between phloem and xylem in the single bundle shown by a broken line (× 32)

FIG. 3. Surface view of upper epidermis of lamina (× 344)

FIG. 4. Spongy tissue of lamina as seen through the lower epidermis (× 344)

FIG. 5. Cross-section of lamina through a lateral vein (× 344)

FIG. 6. Cross-section of collenchyma and adjacent tissue from petiole (× 166)

FIG. 7. Surface view of lower epidermis (× 344)

FIG. 8. Detailed structure of portion of median trace of petiole in cross-section (× 166)

FIG. 9. Thin-walled, sinuous hair from lower side of leaf (× 166)

FIG. 10. Detailed structure of cross-section of lamina (× 344)

FIG. 11. End view of palisade cells as seen through the upper epidermis (× 344)

PLATE XXXIX

FIG. 1–9. Cross-sections showing successive steps in the origin of the petiole and stipule traces. In Figure 1, the three leaf traces are starting to leave the procambium ring. In Figure 3 the three leaf traces have separated from the ring and the branch trace has nearly closed together. In Figure 4, the leaf traces and branch trace are distinct. In Figures 5–9 is shown how the final petiolar and stipular traces come into existence (Figs. 1–4 × 13; 5–9 × 26)

FIG. 10. Final vein ending (× 344)

FIG. 11. Longitudinal section of sieve tubes from petiole (× 584)

FIG. 12. Longitudinal section of collenchyma and adjacent tissues (× 344)

PLATE XL

FIG. 1–7. Series of cross-sections through junction region of the three leaflets showing successive steps in the anastomosing of the petiolar traces and the origin of the three traces of each leaflet stalk (× 13)

FIG. 8. Cross-section through stalk of terminal leaflet, showing three traces and the outline of a prickle. Phloem is stippled, and adjacent fibrous tissue is solid black (× 32)

FIG. 9. Diagram of lamina and petiole in outline

FIG. 10. Diagram showing how the two small, lateral traces become the first lateral veins at the base of each leaflet lamina, and how the median trace gives rise to all other lateral veins

PLATE XXXVIII

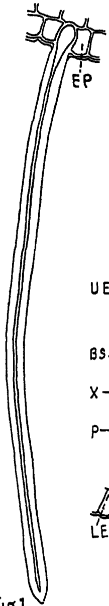
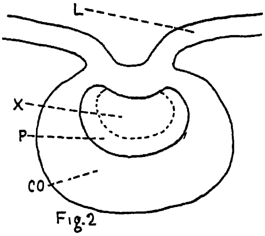


Fig 1



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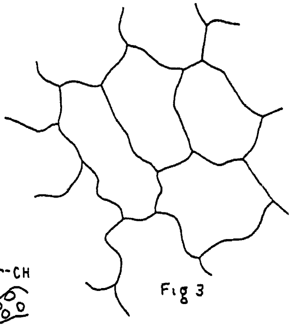


Fig 3

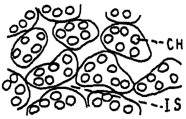


Fig. 4

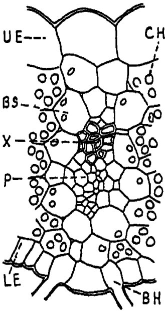


Fig 5

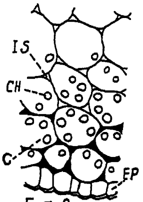


Fig 6

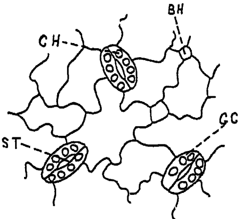


Fig 7

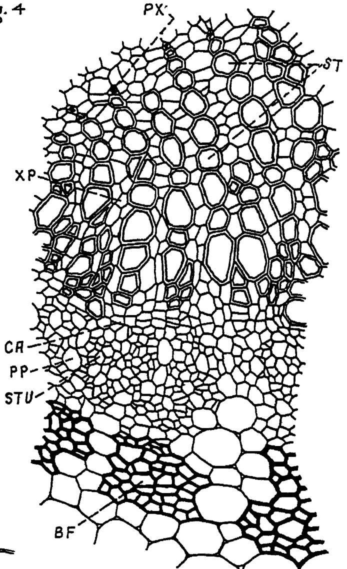


Fig 8

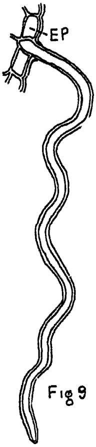


Fig 9

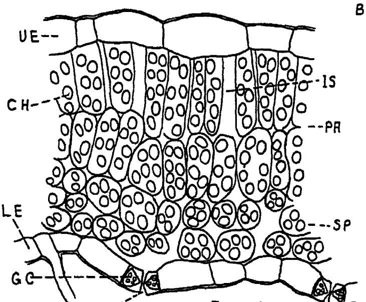


Fig 10

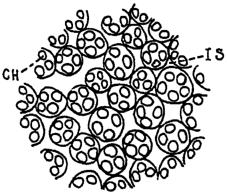
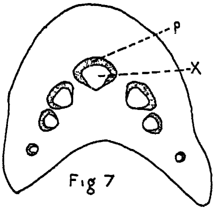


Fig. 11

PLATE XXXIX



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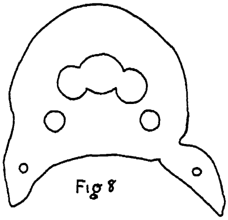


Fig 8

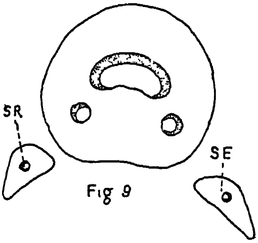
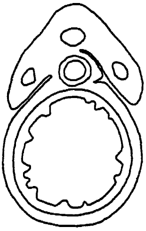


Fig 9



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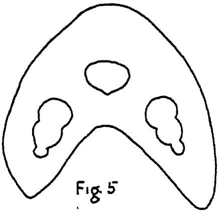

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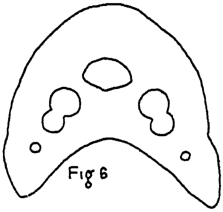

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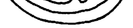

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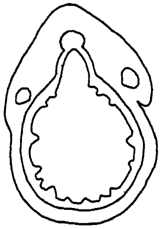

Fig. 2

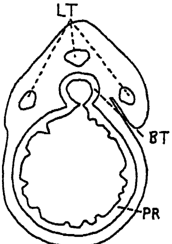

Fig 3

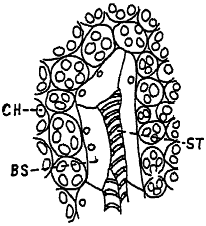

Fig 10

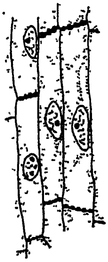

Fig 11

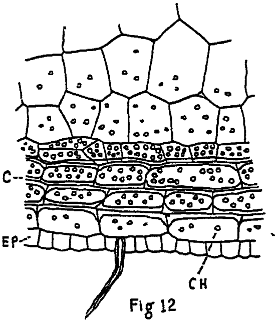

Fig 12

PLATE XL

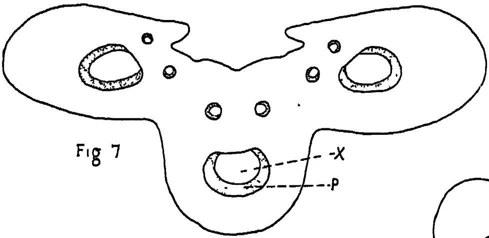

Fig 7

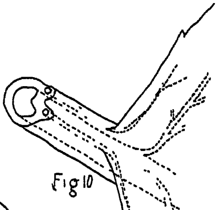

Fig 10

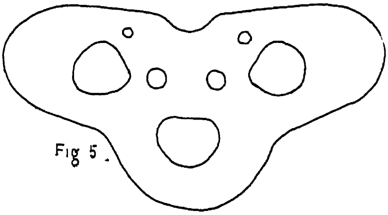

Fig 5

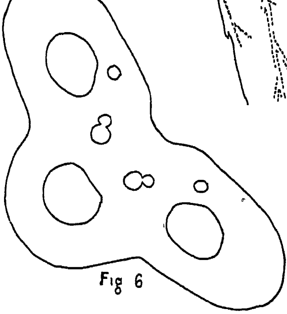

Fig 6

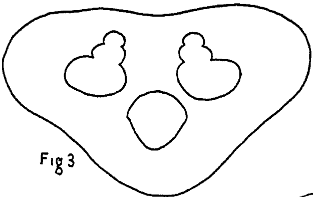

Fig 3

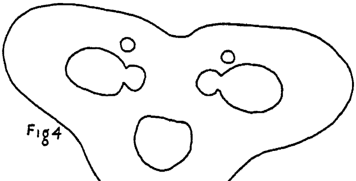

Fig 4

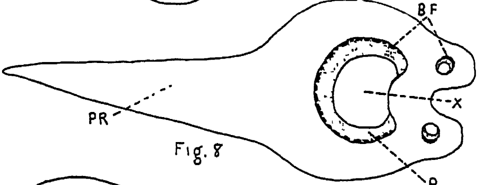

Fig. 8

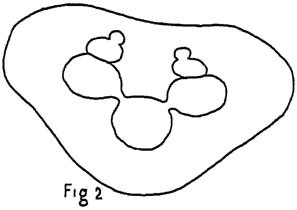

Fig 2

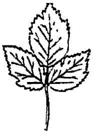

Fig 9

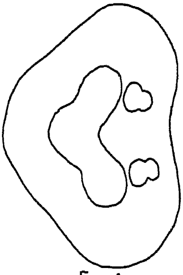

Fig. 1

SEED DEVELOPMENT IN *THELYGONIUM CYNOCRAMBE* L.

EDWARD F. WOODCOCK

THE curved embryo has been considered, by Engler and Prantl (4), to be a character of such common occurrence as to justify the grouping of plants with such an embryo in the Order Centrospermae or Caryophyllales. The serum diagnostic investigations of Malligson (6) seem to bear out the arrangement of Engler and Prantl.

Careful studies of the stages of seed development in several families of this Order have been made by recent investigators. By these studies a more complete knowledge has been gained of the changes occurring in the seed during its development, and the nature of the storage tissue has been definitely determined. Perisperm is the prevailing type in the families thus far investigated, although endosperm is also present in addition to the perisperm in small amounts in several of the families.

Artschwager (1) followed the development of the curved embryo in *Beta vulgaris* L. and found the storage tissue to consist of starchy perisperm with only a small amount of densely granular endosperm in the form of a cap over the radicle of the embryo.

Stevens (7) has shown that the storage tissue in *Fagopyrum esculentum* Moench. is endosperm. The writer has also demonstrated the endosperm in other species of Polygonaceae (8–9), as well as in certain representatives of the Phytolaccaceae (10), Portulacaceae (11), Caryophyllaceae (12–13) and Nyctaginaceae (14). A brief summary of the results of the investigations by the writer will be of interest. The curved embryo was observed to be a prominent character in all the foregoing families. The storage tissue consists entirely of endosperm in the Polygonaceae, the major portion of which is starchy. In the Phytolaccaceae, Portulacaceae and Nyctaginaceae, the storage tissue consists entirely of perisperm. In the Caryophyllaceae the main part of the storage tissue consists of starchy perisperm. In addition to this tissue there is present a cap of protein endosperm about the tip of the radicle.

The results of the investigations which the writer and others are making on the seed development in the different families of the Order Caryophyllales, give a better understanding of the term "endosperm" as used by Bentham and Hooker (2) and Harz (5), and of the word "albumen" as used by Britton and Brown (3).

The present paper follows the seed development in *Thelygonium cynocrambe* L., a member of the Cynocrambaceae and another representative of the Order Caryophyllales.

DESCRIPTION AND DISCUSSION OF THE MORPHOLOGY OF THE SEED

Microtome sections of the seed at various stages of development and stained in Delafield's haematoxylin were used for interpretation of the conditions found during most of the seed morphology. It was also necessary to make hand-sections of mature seeds embedded in paraffin to get a correct understanding of the position of the embryo in the storage tissue.

The pistil of the flower has one ovule and a style which arises at the base of the ovule (Pl. XLI, Fig. 1). The style is easily broken away from the ovary and becomes dislodged very early in seed development. In all the young pistils examined the style had been lost in handling the specimens, and as a result no study was made of its structure. From the base of the style there is evident a stylar canal leading to the ovary cavity (Fig. 2). It is quite probable that this canal also extends into the style. The ovule primordium almost completely fills the ovary cavity, and continues to occupy that position throughout seed development. As the ovule develops, the ovary wall is gradually pushed up and the ovule becomes curved to produce a campylotropous type (Fig. 3). The torus which supports the ovary is as broad as the ellipsoidal, slightly flattened ovary, and is one third as long as the ovary.

The ovule presents some very interesting features in its nucellus and integument development. Not all the early stages of ovule development were available for study, but it is quite probable that, as the ovule comes to be curved as shown in Figure 3, the single thick integument arises from the tip portion of the nucellar tissue, thus forming a long micropylar canal leading to the embryo sac. This method of development is quite unusual, since the integument or integuments usually arise from the bottom of the ovary cavity at about the same time the nucellus originates and, when the ovule is mature, surround the nucellus, except for the micropylar canal. The foregoing suggestion for the integument development in Thelygonium seems to be quite logical, since there is no indication of conducting tissue extending into that portion of the ovule which one would ordinarily consider funiculus, having in mind the place of origin of the integument. The vascular supply to the ovule sends off a branch to the style.

The embryo sac is deeply embedded in the micropylar portion of the nucellus and by the time the embryo has reached the octant stage (Fig. 3) cellular endosperm is evident. As further growth occurs, the embryo sac becomes curved and extends in a central position almost to the chalazal region of the ovule (Pl. XLI, Fig. 3; Pl. XLII, Fig. 6). The sac appears somewhat broadened in cross-section, and curves over the broad central nucellar region. The location of this nucellus is well shown in a cross-section of the mature seed (Pl. XLII, Fig. 10). The embryo, in developing from the octant stage to the stage shown in Plate XLI, Figure 4, first becomes elongated, cylindrical, and almost twice as long as wide, before any well-marked cotyledons are developed (Fig. 5). The two lateral elevations at the end of the embryo in the foregoing figure are the cotyledon primordia, between which appears a rudimentary plumule. The embryo differentiation continues and the various regions become well marked (Pl. XLII, Fig. 6) and the two well-developed cotyledons now make up almost half the embryo. In the further development of the embryo, it becomes somewhat curved to reach the condition shown in Figure 6.

While the embryo is going through these changes, the embryo sac increases in extent and the nucellus dissolves away, except a central sheet, several cells in thickness. There is also present at this time in the ovule a four- or five-celled layer of nucellus between the embryo sac and the surface of the ovule. The outer cells of this layer (Fig. 8) contain numerous, large protein granules which persist as long as the nucellus remains in an undissolved condition. In the stage shown in Figure 6, the cellular endosperm has continued its development until it exists as a several-celled layer in contact with the embryo sac wall. The central region of the sac does not become filled with endosperm and it is down through this region that the embryo gradually proceeds as growth occurs. The cell structure of this endosperm layer is shown in Figure 7. Each of the cells contains a rather large, centrally placed nucleus, small simple starch grains and protein granules. The amount of storage substance is more abundant next to the nucellus than elsewhere in the endosperm.

The structure of the ovary wall and torus, when the seed development has reached the stage shown in Figure 6, is of interest. The cells which form the ovary wall vary greatly in form, as shown in Figure 8. The outer five layers of cells and the single inner layer are much flattened. Between the two regions of flattened cells there is a region of angular cells which are not flattened, and are of importance to the mature fruit since they become thick-walled and form a very efficient protective part of the fruit coat. The basal part of the cortical portion of the torus (Fig. 6) is modified into a fold, the epidermis of which is made up of long broad palisade-like cells.

The mature fruit is brownish-black, and has a very hard pericarp, which almost completely surrounds the single naked seed (Fig. 9). The torus forms the basal part of the fruit as a somewhat knob-like pulpy structure. The only evidence of nucellus in the seed is a thin, papery layer made up of cell remains, which almost completely surrounds the seed, and a central sheet of nucellus several cells in thickness. This sheet extends all the way across the seed (Fig. 10), and extends upward almost to the curve in the embryo (Fig. 9). The endosperm tissue consists of cells in which there are present closely packed, small starch grains and numerous small protein granules (Fig. 11). The curved embryo occupies a central position in the endosperm tissue and consists of flattened, narrow cotyledons which are almost three times as wide as the diameter of the cylindrical radicle and hypocotyl and also somewhat shorter. This is well shown in Figure 10, as is also the shape of the cavity in which the radicle is located. The plumule is evident as a slight elevation at the base of the cotyledons.

SUMMARY AND CONCLUSIONS

The ovule of *Thelygonium cynocrambe* L. is compylotropous and completely fills the ovary cavity. The single thick integument is of unusual interest in its development, since it originates from the terminal portion of the nucellus as it becomes curved, and does not inclose the nucellus, as usually happens. The curved embryo, which is surrounded by endosperm, has a cylindrical radicle and hypocotyl and narrow, flattened cotyledons. The torus forms a knob-like structure at the base of the fruit, and remains attached when the fruit is shed. The developmental studies of the seed in Thelygonium establish the true nature of the storage tissue as endosperm.

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PLATE XLI

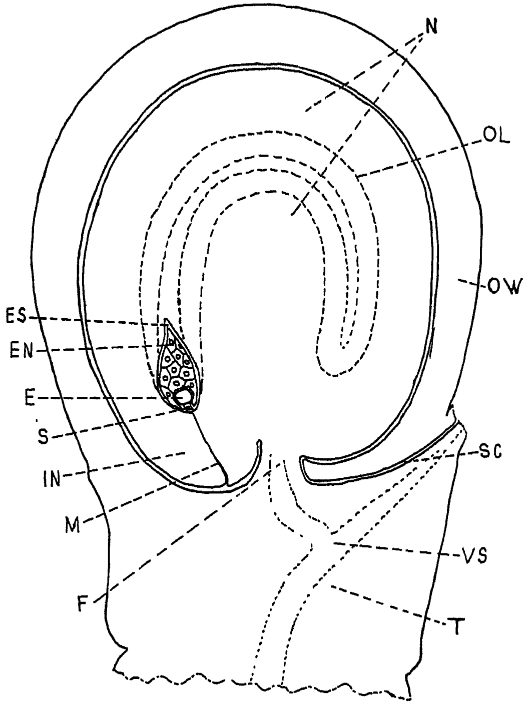


Fig 3

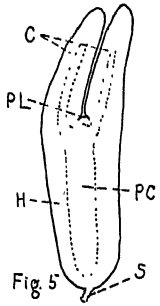


Fig. 5

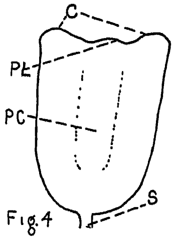


Fig. 4

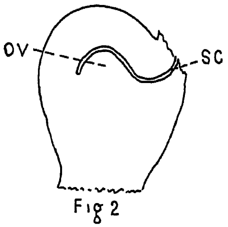


Fig 2

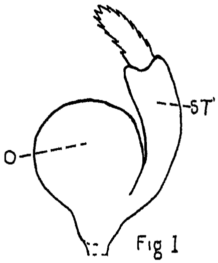
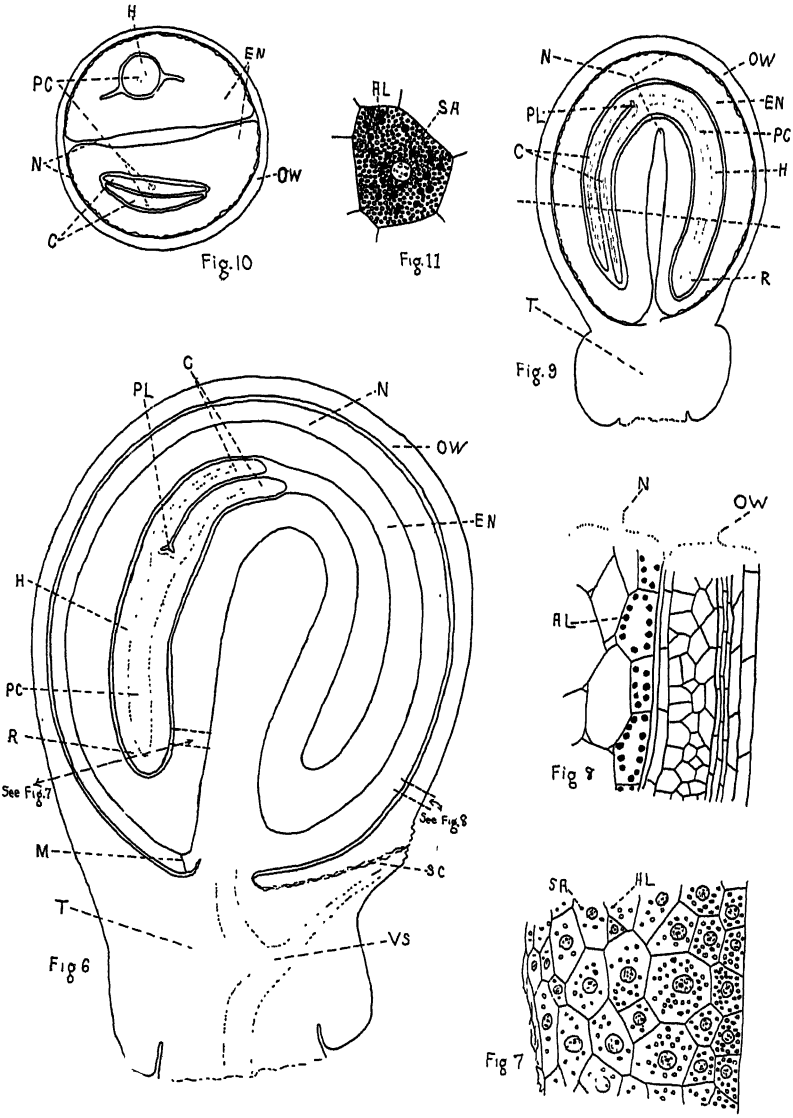


Fig 1

Seed of *Thelygonium cynocrambe* L.

PLATE XLII



Seed of *Thelygonium cynocrambe* L.

DESCRIPTION OF PLATES XLI–XLII

Seed of *Thelygonium cynocrambe* L.

All figures drawn with aid of camera lucida from median longitudinal sections except Figure 10, which is a cross-section, and Figure 1, which is from Engler and Prantl. The following abbreviations are used: EN, endosperm; E, embryo; S, suspensor; IN, integument; M, micropyle; F, funiculus; OL, outline of embryo sac; OW, ovary wall; SC, stylar canal; VS, vascular strand; C, cotyledon; PL, plumule; H, hypocotyl; PC, procambium; OV ovule; ST, style; O, ovary; N, nucellus; AL, protein granule; SA, starch grain; T, torus; ES, embryo sac; R, radicle.

PLATE XLI

FIG. 1. Side view of very young ovule showing the basal attachment of the style (after Engler and Prantl)

FIG. 2. Young ovary, showing origin of ovule primordium, and stylar canal. The style has been torn away (× 60)

FIG. 3. Young ovary in which the ovule has become sufficiently developed to show its campylotropous nature, and its single terminal integument. The cellular endosperm surrounds the spherical embryo. The broken line indicates the position which the embryo sac with its lining of cellular endosperm will take (× 60)

FIG. 4. Embryo showing first indications of cotyledons and plumule (× 60)

FIG. 5. Later stage in embryo development showing well-delevoped cotyledons and plumule (× 32)

PLATE XLII

FIG. 6. Half-mature fruit showing embryo, nucellus and large embryo sac with its layer of endosperm and its embryo located in the median cavity (× 26)

FIG. 7. Cellular endosperm from stage shown in Figure 6. Small starch and protein grains evident (× 166)

FIG. 8. Detail of ovary wall and adjacent nucellus from stage shown in Figure 6. Protein grains seen in outer layer of nucellus (× 166)

FIG. 9. Mature fruit showing the thick pericarp and papery remains of nucellus. The curved embryo is entirely surrounded by endosperm. Broken line across figure shows plane of cross-section shown in Figure 10 (× 13)

FIG. 10. Cross-section of mature fruit, showing shape of embryo, and endosperm surrounding the embryo (× 13)

FIG. 11. Single cell from endosperm of mature seed, showing the cell lumen filled with closely packed, small, simple starch grains and occasional protein grains (× 166)

THE EXPERIMENTAL DETERMINATION OF AN INVISIBLE MUTATION *

JOHN J. BITTNER

INTRODUCTION

THE tumor employed in the present experiment arose spontaneously in an individual of a homogeneous stock of mice known as the dilute browns in Dr. L. C. Strong's laboratory of the University of Michigan. It was diagnosed as an adeno-carcinoma of the mammary gland and given the symbol *dBrB*.

For the past ten years this neoplasm has been continued by the process of transplantation. During this time it has been inoculated into several hundred (approximately 500) of the dilute brown mice, with the result that all the individuals grew the mass progressively on the first inoculation.

Owing to the small number of mice available from the parent stock of dilute browns, the tumor has been kept growing for the past year by means of inoculation into members of another branch of dilute browns secured from Dr. William S. Murray. These mice are directly descended from the so-called parent strain. Experimental determination showed that some of the inoculated individuals refused to grow the transplant — a phenomenon never encountered in the use of Strong's derivative of the dilute browns.

METHOD AND DATA

The trochar method of inoculation was employed throughout this experiment. All transplants were placed in the region of the right axilla, where an abundant supply of blood was available.

Of 341 individuals secured from Dr. Murray, 67 proved to be negative on the first inoculation. They were not reinoculated.

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* From the Department of Mammal Genetics, University of Michigan.

At first it was thought that the failure to grow the transplanted neoplasm was due to failure in technique, but this supposition was discarded owing to the large number of negative mice. It is quite possible that some of the negative animals would have grown the transplant upon a second inoculation. On comparing the results with other experiments performed at the same time, in which all the individuals grew the transplanted mass progressively, the conclusion arrived at was that the difference in susceptibility to the transplant was inherent within the individuals. A tabulation of these comparative data is given in Table I.

TABLE I

Tumor, dBrB (Adeno-carcinoma)		
dBr Stock	Strong's derivative	Murray's derivative
+	500 (app.)	274
−	0	67
Percentage +	100	80.35 ± 4.89

HISTORY OF THE DILUTE BROWN STOCK

Before going on, it will be best to give a short history of the stock of mice in question. Their inbreeding was begun by Dr. C. C. Little in 1909. In 1919 Dr. Little transferred his colony to Dr. Strong, who returned part of the stock to Dr. Little a year later. Dr. Murray assumed charge of Little's stock in 1925. Brother-to-sister matings have been employed in all stocks from the beginning.

The sublines have thus been separated since 1920. During this time they have been subjected to different environmental conditions and have had different diets.

DISCUSSION

By an extensive investigation covering a period of many years and the employment of several thousand experimental animals, Strong has developed the theory "that the fate of the implanted tumor tissue in a given individual host is brought about by a reaction between the host, determined to a large extent by its genetic constitution, and the transplanted tumor cell, controlled to some extent by certain intrinsic factors" (1). This theory has withstood the tests of rigid verification.

From the data obtained in the present investigation, it is evident that a change has taken place either within the tumor cell or within the mice. It is quite certain that the change in constitution did not occur within the tumor.

The other alternative is that a change has occurred within the genetic constitution of one or more of the mice, which, by the continued inbreeding of the stock of dilute browns now in Dr. Murray's laboratory, has given rise to a mutation among the factors which determine susceptibility to transplantable cancer. In other words, the reaction potential between the transplanted tumor and the host has not remained constant.

The pedigree of most of the mice inoculated in this experiment is not available, since the original purpose was merely to keep the tumor alive. From the data secured from the inoculation of about 60 mice, the pedigrees of which are known, it appears as if negative individuals were grouped according to litters and the same thing is true for positive animals. Thus it would seem as if the change in reaction to the tumor is confined to one or more of the side lines of Dr. Murray's stock. In the future, care will be taken to secure the pedigree of every individual and to determine, if possible, in what line or lines the mutation is perpetuated at the present time.

UNIVERSITY OF MICHIGAN

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INTERSEXUALITY IN TADPOLES OF *RANA CANTABRIGENSIS* *

TSO-HSIN CHENG

INTERSEXUALITY, briefly defined, is a state of hermaphroditism in dioecious species, regardless of its being functional or rudimentary, temporary or persisting, germinal or otherwise. Much has been written about Pflüger's hermaphroditism in frogs, which appears to be of normal occurrence in the so-called undifferentiated races. In frog tadpoles of the differentiated races, however, records of intersexuality are surprisingly rare. The writer has recently accumulated some data on juvenile intersexuality in the strain of *Rana cantabrigensis* at Ann Arbor, Michigan. Analysis of these data may throw some light on certain fundamental problems relating to hermaphroditism and sex reversal as well as to normal sexuality.

The writer wishes to express his gratitude to Professor Peter Okkelberg for advice and unfailing interest in his work.

MATERIALS

In the spring of 1928, several hundred wood-frog tadpoles, obtained from normally fertilized eggs, were raised in the laboratory. They were fed on water plants and hard-boiled egg yolk, and kept in oxygenated water, with the surrounding air temperature fluctuating between 15 and 25 degrees Centigrade. The tadpoles were active and healthy and mortality was low.

A few animals were killed and fixed at twelve or twenty-four hour intervals. For fixation, various reagents were employed, of which Zenker's and Bouin's fluids were most frequently used. In dissecting out the gonads, the mesonephros was usually left attached to them. The material was then sectioned serially at 6, 8 or 10 micra, and stained with Heidenhain's iron hematoxylin. Of all the gonads so far studied, about 300 specimens are far enough advanced to be sexed. Their sex ratio is approximately 1 : 1, with neither one nor the other sex predominating in number in any particular period of sex differentiation. Male and female gonads are developed early, and are typical testes and ovaries, exhibiting none of the peculiarities characteristic of the gonads of the undifferentiated races. The nine intersexual tadpoles to be described below are distinct exceptions.

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* Contribution from the Zoölogical Laboratory of the University of Michigan.

DESCRIPTION

Case 1 (Pl. XLIII, Fig. 1). — This larva is 105 days old,[1] with a total length of 40.5 mm.; fore-limbs not externally visible, hind-limbs well developed.

Both genital glands are testis-like in size and appearance. The left gonad is approximately 0.6 mm. in length; the right one is only two thirds as long. Upon sectioning, the right gonad is found to be a normal testis with the exception of two masses of an intensely stained substance, which are probably degenerating ova. A network of rete tubules is distinct, connecting the testis ampullae with the vasa efferentia. The left gonad is intersexual to a high degree.[2] It is mainly testicular posteriorly and ovarian anteriorly. The testicular tissue predominates in quantity and shows, in different places, a tendency to ampulla formation. The ovarian substance is composed of large cells, measuring in some cases over 100 micra, and closely resembling oöcytes of the second growth period. Most of these oviform cells are structurally abnormal, exhibiting various signs of degeneracy. The process of degeneration is undoubtedly associated with profound physiological changes in the protoplasmic materials. The oöplasm turns more intensely basophilic than usual, and coincidently, the nucleoli, normally spheroidal and condensed, rapidly multiply and hypertrophy at times into masses of unusual size and of peculiar shape. Along with the nucleolar hypertrophy, chromophilic bodies of a different origin may also make their appearance in the nucleus. Subsequent to these changes, the egg cell undergoes a gradual resorption, the cellular elements diminishing and disappearing until finally only a dark-stained agglomeration of the nuclear materials is retained. Such detritus forms the last remnants of an ovum and may persist for some time before its complete deterioration. During the entire process the egg follicle undergoes reduction in size, generally, but not always, in proportion to the degree of cell degeneration, and eventually disappears with the dissolution of the ovum.

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[1] Age of tadpoles is calculated from the time of egg laying.

[2] The gonad is here designated as intersexual merely for convenience of description. The sexual nature of the "ovarian" substance in this gonad will be discussed later.

The few oöcytes distributed throughout the testicular portion of this intersexual gonad show essentially similar degeneration phenomena. The chromatin materials, normally oxyphilous during this period of secondary growth, here assume a basophilic nature, appearing as dark, plumous threads with many granules on them. The nucleus is distinctly enlarged relatively to the scanty and diminishing amount of oöplasm. The follicular membrane is generally indistinguishable as such. In some cases there appears an actual invasion of spermatogonial cells and stromal tissue into the degenerating ova.

Case 2 (Pl. XLIII, Fig. 2). — This larva is 77 days old, with a total length of 42 mm.; fore-limbs not externally visible, hind-limbs about 8 mm.long.

On external examination, both gonads appear as testes. The right gonad is larger, measuring about 0.5 mm. in length; the left gonad is only 0.3 mm. long. Microscopically the right genital gland shows no deviation whatsoever from the typical male gonad. The left gland contains a score of large cells scattered throughout an otherwise normal testicular tissue. These cells look like rudimentary oöcytes of the second growth, with a mean diameter of 35–40 micra. In the nucleus, the most striking features are large spheroidal bodies, staining intensely black. Many of these peculiar bodies are aggregated along the periphery and adhere to the nuclear membrane; some are even extruded into the cytoplasm. Frequently the nuclear membrane becomes indistinguishable; consequently, all the black nuclear débris appears to lie imbedded in the cytoplasm itself. This whole structure is unquestionably in a process of degeneration, and is doomed for ultimate resorption. The follicular membrane is absent, or at any rate is too indistinct to be identified. Two or more of the ovum-like cells often unite to form a multinucleated structure.

Case 3 (Pl. XLIII, Fig. 3). — This larva is 70 days old; body measures 35 mm. in length, with a persistent tail of 21 mm.; both fore- and hind-limbs are developed.

The left gonad has a length of 256 μ, a width of 400 μ and a thickness of 164 μ.[3] Spermatogonia are found in great numbers. Among them are scattered many maturation cells, most of which are undergoing early synaptic changes, while others appear as degenerating ova. The latter cells are characterized by very scanty cytoplasm and many basophilic bodies in the nucleus. These bodies increase in size and number as the cells degenerate (see case 2). From all evidence, they appear to be more than mere accumulations of waste materials, being actually a characteristic morphological manifestation of a most profound derangement of cellular life, which leads to degeneration.

The right gonad measures 400 μ in length by 260 μ in width and 230 μ in thickness. Like the left gonad, it is an abnormal testis, containing a number of maturation cells. Leptotene, pachytene and synizetic nuclei are generally confined to the peripheral region, and are frequently badly distorted by overcrowding. Ovum-like cells are present as small abortive structures. A few of them attain a fairly good size, with a maximal diameter of about 60 micra, and are inclosed in follicles.

This tadpole was raised with a group of others in a temperature of 25° ± 3° C. Most of the tadpoles were fixed before sex could be recognized. The sex ratio of those killed subsequent to morphological sex differentiation is tabulated on the opposite page.

Our data give no evidence that intersexuality in this case is a result of increased temperature, but the small number of specimens here involved is insufficient to warrant any positive conclusion on this point.

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[3] All dimensions of the gonads are given at maximum value, unless otherwise stated.

Age	Number of specimens Male	Female
25 days	1	0
41 "	1	3
43 "	1	1
48 "	2	1
70 "	1	1 (and one intersex)
76 "	2	1
	8	7

Case 4 (Pl. XLIV, Fig. 1).—This larva is 69 days old, measuring 45 mm. in length; fore-limbs not externally visible, hind-limbs about 5 mm. long.

The left gonad appears to be of the ovarian type, measuring 640 × 560 × 240 micra. The germ cells are grouped around a central ovarian cavity. Oögonia and young oöcytes of the synaptic phase,[4] either massed or single, assume a peripheral position, lying close against the peritoneum of the gonad. Large growth cells, each surrounded by a delicate follicle and containing in the nucleus an almost oxyphilous chromatin network and many spherical and condensed nucleoli are generally found in the deeper layer of the cortex. Rete-cord material appears quite dense near the mesovarial attachment, and is relatively scanty elsewhere. The lumen of the central cavity is frequently obliterated by the inward crowding of the growing auxocytes. Careful study of the entire gland has revealed no sign of degenerative activity.

The right gonad is an ovum-containing testis. It measures 350 × 380 × 200 micra, being considerably smaller than the left gonad. Rete-cord cells are abundant, with numerous spermatogonia scattered throughout. A number of oöcytes in the first and second growth are found imbedded among the testicular structures, and are enveloped by actively growing spermatic tissue.

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[4] Maturation stages in the first growth have frequently been referred to as "pseudoreduction stages," for which term Witschi has recently substituted "prereduction stages." Witschi's terminology may cause some confusion, for the term "pre-reduction" has been defined as "chromosome-reduction in the first instead of the second meiotic division" (Wilson). The writer prefers to designate the period of first growth as "synaptic phase" or "synaptic period."

Large oöcytes measure from 40 to 60 micra in diameter. They appear devoid of any follicular membrane, their oöplasm being sometimes invaded by surrounding cells; their nuclei, however, are intact, exhibiting no sign of morphological abnormality.

Case 5 (Pl. XLIV, Fig. 2). — This larva is 62 days old; body measures 38 mm. in length, with well-developed hind-limbs and a badly crooked tail. The two gonads are similar in form as well as in size, measuring approximately 780 × 180 × 160 micra. In structure, the right gonad is a normal testis; the left one is mainly testicular, containing, however, in its posterior half scores of sex cells in abortive oögenesis. Many of the oöcytes are in the early stages of maturation, characterized by the formation of much coiled and tangled spiremes in the nucleus. Some oöcytes have apparently entered the second growth period. They measure 30–40 micra in diameter, being approximately one third smaller than normal ova in this period of germ-cell development.

The maturation cells are generally grouped around the gonad periphery, and are in some places so abundant that they become aggregated in several layers in the form of a stratified germinal epithelium. In these places rete-cord cells are scanty and scattered; elsewhere they are dense and in active condition. Spermatogonia are found associated with the rete-cord elements and appear normal in every respect.

Case 6 (Pl. XLIV, Fig. 3). — A larva 55 days old. It is obviously underdeveloped, measuring only 15.5 mm. in total length. Normal tadpoles of this age are over 30 mm. long, with well-developed hind-limbs.

The sex organs are small. In the left gonad, the anterior third has the structure of a compact testis, the middle third is mainly testicular, containing some maturation cells; the posterior third looks like an early female gland, with distinct ovarial sacs, around which are found many "nests" of maturation cells among the gonia. In the right gonad, the anterior two thirds are testicular; the posterior third is similar to the corresponding portion of the left gonad in containing an ovarian cavity and numerous maturation cells, both of which features are characteristic of the young female gland.

The maturation cells are recognized by the much intertwined nuclear threads, either in loose spireme formation or in a more or less condensed mass. Intermediate stages showing gradual condensation of the nuclear content to complete synizesis can be arranged in proper sequence.

Case 7. — A larva 51 days old and 28 mm. long. The left gonad attains a length of 800 μ, with a mean thickness and width between 130–150 μ. The right gonad is on the average approximately one fourth smaller in all dimensions. Histologically, both gonads show similar features. Anteriorly, the gonadic structure is typically testicular. Rete cords are thoroughly dispersed among the spermatogonial cells, giving to the structure an appearance of compactness and uniformity. In tracing the sections backwards, maturation spiremes soon begin to make their appearance. These increase in number posteriorly, being aggregated peripherally, with the spermatogonia confined to the central mass of rete cords. Any section through this region of the gonads presents a striking combination of elements of both sexes. Further back still, the spermatogonia disappear altogether, the rete-cord material becomes reduced in amount, and the gonads assume pure female characteristics. The oöcytes are in various stages of early maturation exactly coinciding with those maturation stages as found in typical ovaries at this period of sex differentiation. Both testicular and ovarian elements are morphologically typical, appearing as normal developing structures.

Case 8. — A larva 51 days old, measuring 34 mm. in length. The left gonad is a normal testis with no unusual feature. The right gonad contains for the anterior one fourth of its total length follicles of maturation cells, which are localized at the distal periphery. Elsewhere, the germinal tissue is testicular and typically so. The maturation cells are in the synaptic period, showing no sign of second growth, nor any indication of regressive changes.

Case 9. — A larva 38 days old, and 25.5 mm. long. Both sex organs are small. The left gonad has a normal testicular structure anteriorly; posteriorly it still remains morphologically undifferentiated. The primary genital cavity with characteristic embryonic connective tissue is in evidence. Prominent rete cords are found projecting into the gland at regular intervals. The right gonad is testicular anteriorly and ovarian posteriorly. In the testis portion, the rete cords are compact and spermatogonia numerous. The ovary portion contains in the cortex many oögonial cells and young oöcytes in the form of "egg-nests." Segmentally arranged rete cords are confined to the medulla, in which no germ cells have been detected. The testicular and ovarian portions are by no means distinct; the sexual substance of both portions is intermingled along the region of junction.

DIAGNOSIS OF SEX

For diagnosis of sex in our present material, only morphological criteria are available. Since in most of the cases described there is hardly any trace of extragonadal sex characters, we have to base our sexing chiefly upon the characteristics of the germ cells and upon the internal as well as the external structure of the gonads. These two features are associated phenomena in the normal process of sex differentiation. Discussion of any one naturally calls for a due consideration of the other.

A. Sexual characteristics of the germ cells

1. Ovum-like cells.—The sex of the ovum-like germ cells in frogs has been a question of much debate. They have often been described and identified as true ova. Levy (1920), however, claims that "die von Pflüger, Born, Friedmann, Kuschakewitsch, Witschi u. a. beschriebenen Eier keine Eier, sondern polyploide Riesenzellen darstellen." This view is also held by Orlowski (1925). Champy (1913) derives the oviform germ cells from the degenerative hypertrophy of the primitive gonia in the male gonad. Swingle has contended that the oöcyte-like cells are not necessarily female cells, but may be merely male germ cells undergoing oviform degeneration in the course of a precocious and abortive sexual cycle. Crew and Fell (1922) have found in an ectopic testis of a frog many ovum-like bodies, which, they believe, are formed by the liquefaction of the spermatozoa. These various interpretations are sufficient indications that an oviform appearance alone is by no means an absolute sex criterion. For the sexing of ovum-like germ cells, we have to resort to their morphological organization, and particularly their genesis and developmental history.

In our material, ovum-like germ cells, except those in degeneration, have the characteristic structure of true ova. In cases 3, 4 and 5, they are actually shown to have been derived by a normal oögenesis. The germ cells undergo all stages of the synaptic phase, i.e., leptotene, synizesis and pachytene, and subsequently enter the second growth period. A seriation of these maturation phenomena in an embryonic gonad is unmistakably a female characteristic. In cases 1 and 2, there is no trace of synaptic figures, and most of the "oöcytes" or ovum-like cells are morphologically abnormal and degenerating. The sex of these cells is, therefore, problematical. If, however, we consider these cases in the light of sex reversal, the probability becomes evident that these ovum-like cells may be the remains of a normal ovarian tissue. In response to a tendency of gonadic masculination, the young oöcytes have become completely destroyed and resorbed, while the growing·auxocytes, being more resistant to adverse conditions than their progenitors, consequently degenerate more slowly. There is little doubt that these degenerating ovum-like cells will eventually degenerate completely and disappear.

2. Cells in synaptic phases of maturation. — The occurrence of early maturation cells in a sexually abnormal larval gonad, and especially in an otherwise normal juvenile testis, reminds one of a phenomenon described in other frogs as prespermatogenesis. This phenomenon has been reported by Champy (1913) in *Rana esculenta,* Witschi (1921), in *Rana temporaria,* Allen (1918), in thyroidectomized *Rana pipiens,* Hoskins and Hoskins (1919), in thyroidectomized *Rana sylvatica.* Swingle argues that in *Rana catesbeiana* male maturation cycle occurs annually, beginning with the first year of larval life. He has found numerous sperms in the gonads of metamorphosing and recently metamorphosed bullfrogs of both differentiated and undifferentiated races. He has also found sperms in the testes of small, immature leopard frogs (see also Parmenter, 1925) and stated (1921, 1922) that tadpoles of this species and of other species with short larval life might undergo a precocious and abbreviated maturation cycle very early in development. Later (1923), he expressed his belief that "races with direct testis formation undergo an abortive post-larval sexual cycle culminating in degeneration of male sex products."

In our wood-frogs, normal larvae do not undergo any precocious male maturation cycles. Examination of numerous tadpoles reveals no sign of so-called prespermatogenesis. The early maturation cells already described cannot be regarded as male cells in abortive maturation, but are identical with normal female cells. The evidence for this point of view is quite conclusive: (*a*) in cases 6, 7, 8 and 9, all maturation stages are strikingly similar to those in the typical ovary of tadpoles of the same age; (*b*) all the maturation cells are aggregated in the cortical portion of the gonad, usually inclosing a central cavity, as in the young ovary: (*c*) these maturation cells do not always degenerate, as inferred from their morphology, and do not undergo meiotic divisions, which would occur in case of spermatogenesis, but enter the second growth period, as seen in cases 3, 4 and 5.

Swingle (1926) has observed cells of the synaptic phase in larval testes of *Rana catesbeiana*, for which abnormality, however, he has offered no explanation. In *Rana sylvatica*, Witschi (1929) has recorded the occurrence of early maturation cells in an otherwise normal testis. The formation of such an hermaphroditic gonad is ascribed as being due to a failure of some of the primordial germ cells to reach the medulla in proper time. The latter phenomenon evidently cannot be considered as the initial cause of intersexuality. It is merely an expression of, or a response to, a predetermined hermaphroditic nature. Witschi also claims that the oöcytes in the young hermaphrodite gonad degenerate very soon, but our data show that they may persist for a considerable period.

3. Gonial cells. — The primitive gonia, once sexually differentiated, become either oögonia or spermatogonia. In the larval gonad, the oögonia aggregate peripherally and soon begin to mature, while the spermatogonia pass to the rete-cord region, where they remain in multiplication usually for a long period. Hence, the formation of a surface germinal epithelium is a female feature, whereas the migration of the germ cells into the rete cords may be regarded as indicative of a male condition.

Relying on these fundamental facts, Witschi has formulated his theory of localized sex-differentiators. He assigns the male-differentiating properties to the medulla and the female-differentiating properties to the deeper layers of the cortex. Swingle (1922), however, argues that "It is in the region of the most marked 'female' tendencies that the writer finds in the bullfrog entire cysts of unmistakable spermatocytes, and occasional spermatids." In our material, it happens frequently that the oöcytes are found scattered throughout and imbedded in the testicular substance. Such condition may conceivably indicate that the ovarian cells, normally differentiated in the germinal epithelium, may in abnormal cases become differentiated elsewhere in the gonad. However that may be, it actually demonstrates the fact that the female sex cells, once differentiated as such, remain as such no matter where in the gonad they may happen to be located. They may degenerate, of course, but under favorable conditions they may continue to develop and form typical testis-ova, as recorded in many cases of intersexual frogs.

B. Morphology of the gonads

The outside appearance of the gonads in early stages of sex differentiation shows no definite sex characteristics. In later stages, all the intersexual gonads are testicular in appearance, being small, narrow and retaining a fairly regular outline. In contrast to this, the ovary is large, broad and much folded and wrinkled.

With regard to the internal structure, the young testis is compact and homogeneous, with many spermatogonial cells distributed evenly throughout and imbedded in the rete-cord material, which later gives rise to the rete apparatus. The larval ovary, on the other hand, is characterized by a thickened germinal epithelium inclosing ovarial sacs. In studying our material in the light of this basic difference, it becomes apparent that the young intersexual gonad generally possesses distinct components of both ovarian and testicular structures, and that the older intersexual gonad is invariably testicular in structure, or at least mainly so.

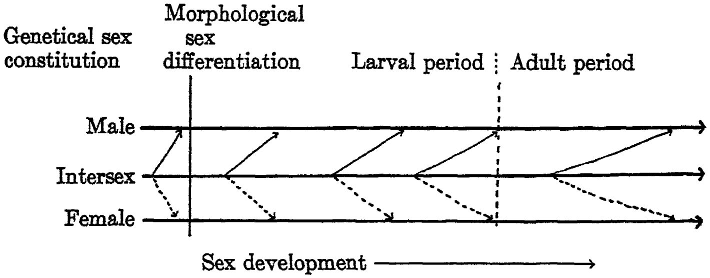
Thus the external as well as internal morphological features of the intersexual gonads suggest an increasing prevalence of the male characteristics in these gonads relatively to the time of development. Such a condition seems to indicate a sex transformation toward maleness.

ORIGIN OF INTERSEXUALITY

(*A*) Intersexual frogs have often been regarded as intermediate forms in the process of sex reversal, and external environmental agencies have been postulated as causative factors of sex reversal. In our experiments, however, all tadpoles, except those kept at a high temperature, were raised under practically identical conditions. The appearance of a few intersexual forms here makes one doubtful regarding the influence of external environment in producing these intersexes. Even those tadpoles raised at a high temperature do not seem to show that the increased temperature bears any causal relationship to the genesis of intersexuality.

(*B*) Intersexuality here may be of the same nature as that existing in Pflüger's hermaphroditism. It has been definitely acknowledged by investigators generally that Pflüger's hermaphrodites are not true hermaphrodites. Witschi (1923) states that "die Juvenilhermaphroditen genetische Männchen mit der Rudiment der weiblichen (ersten) Phase sind." Swingle (1926) concludes that Pflüger's hermaphrodites are genetic males, exhibiting in the course of larval development a transitory sexually neutral phase. It is feasible to assume that our intersexes also may be genetically pure in sex, but, owing to certain disturbances of the initial process of sex differentiation, characteristics of the opposite sex make their appearance during larval development. If this is so, it seems plausible that Pflüger's hermaphroditism, which occurs normally in the undifferentiated races, may appear in the differentiated races as an abnormality.

(*C*) Intersexuality may be of germinal origin. Our present knowledge indicates that the sex structures of an organism, like any other character, are susceptible to germinal or genetical irregularities. As shown in our data, the intersexual condition has been traced back to a very early stage of sex differentiation when male and female individuals are barely recognizable. This hints at a possibility that our intersexes may have been such from the beginning of sex development. The idea may be represented by a diagram as follows:



Some points of interest may be briefly considered:

(1) It has been a prevalent idea that intersexuality is merely an arrested sex reversal, or an intermediate stage in the process of complete reversal. The probability that sex reversal itself may be induced by an initial state of intersexuality, is frequently overlooked. An incipient intersexual condition may owe its existence to a genetical defect of either the sex primordium in the zygote or the embryonic differentiating factors of sex. Such a defect would result in an incompleteness of dominance of one sex over the other, and the extent of this incompleteness determines the degree of intersexuality. Any factor, be it internal or external, endogenous or exogenous, that alters the relationship of dominancy and recessiveness of the two sexes, may initiate a process of sex transformation, which may gradually proceed to its final completion. It is undeniable that, under certain circumstances, larval intersexuality may persist for a considerable time, leading to a state of adult hermaphroditism (Cheng, 1929).

(2) The diagram implies that sex transformation in the intersexual frogs may occur in the direction of either sex. But in the mass of intersexual material so far studied, it is always the ovarian elements which show developmental abnormality, as in cases 1, 2 and others. This is most convincing evidence that in these cases sex transformation has proceeded in a male direction. Our present data, however, do not preclude the possibility of a sex transformation in the opposite direction.

(3) To ascertain a genetical basis for intersexuality, breeding experiments furnish the most satisfactory means. As far as the writer is aware, breeding of intersexual frogs has been performed in only two instances (Crew, 1921; Witschi, 1923). Both claim that their intersexual frogs are "somatic" males, i.e., masculinized genetic females. But it is necessary to note that their results are concerned only with the F_1 generation. There is always a question whether or not the sexual nature of the F_1 individuals is genetically pure and normal. If the factors or factor-complexes which control the production of intersexes are recessive in nature, only through inbreeding for successive generations can the real genetical sex constitution of the intersexual frog be revealed. In Witschi's self-fertilization experiment (Hh), the great mortality of the F_1 offspring and the occurrence of an hermaphrodite among the remaining individuals are suggestive facts which cannot be overlooked in considering the result of his experiment and the conclusions derived therefrom.

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EXPLANATION OF PLATES XLIII–XLIV

PLATE XLIII

FIG. 1. A transection of the gonads of case 1, showing the various signs of degeneration of the oviform cells in the left gonad. Magnification approximately × 75

FIG. 2. A transection of the gonads of case 2. Note in the left gonad two ovum-like cells and the empty spaces, which are the extreme ends of the follicles that contain degenerate "ova." Magnification approximately × 80

FIG. 3. A transection of the right intersexual gonad (case 3). Magnification approximately × 130. Under higher magnification, maturing cells in the synaptic phase of oögenesis are seen scattered along the gonad periphery

PLATE XLIV

FIG. 1. A transection of the gonads of case 4. In the left ovary, the increased amount of interstitium near the hilus region may be suggestive of an incipient male condition. The right ovotestis contains numerous oöcytes, some of which can be seen along the medial border of the gonad. Magnification approximately × 80

FIG. 2. A transection of the gonads of case 5, showing maturation cells in the left gonad. Magnification approximately × 230

FIG. 3. A transection through the middle of the intersexual gonads of case 6, showing a testis portion in the right gonad, and an ovary portion in the left. Magnification approximately × 300

PLATE XLIII

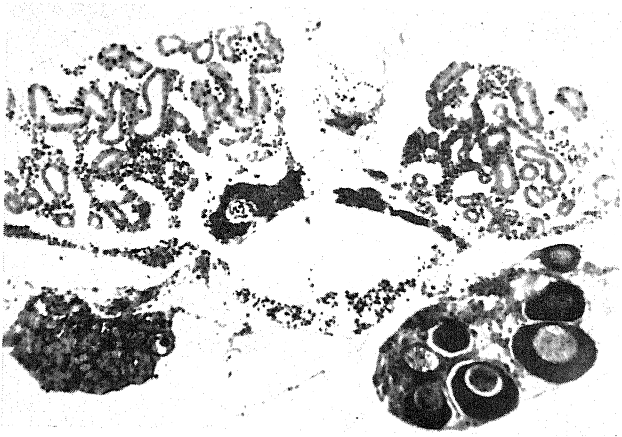

FIG. 1

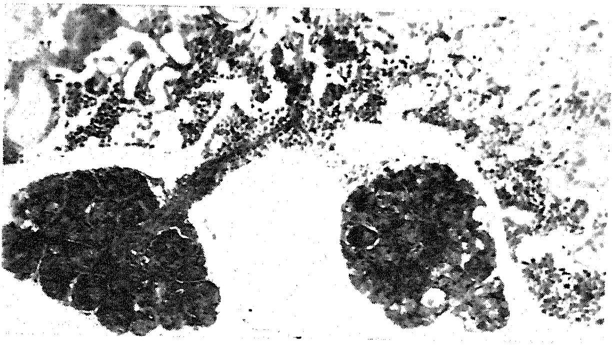

FIG. 2

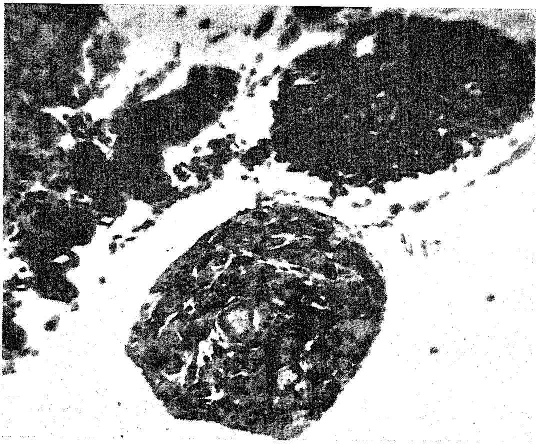

FIG. 3

PLATE XLIV

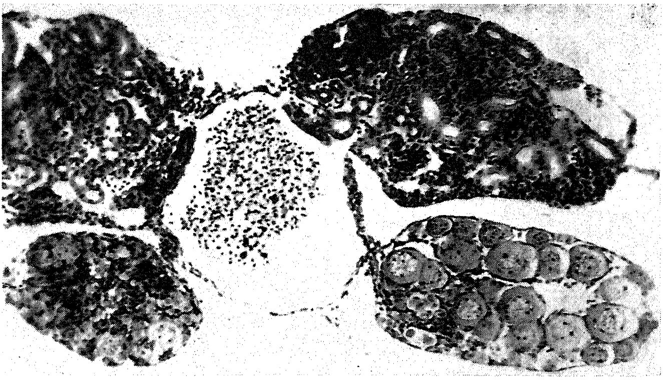

FIG. 1

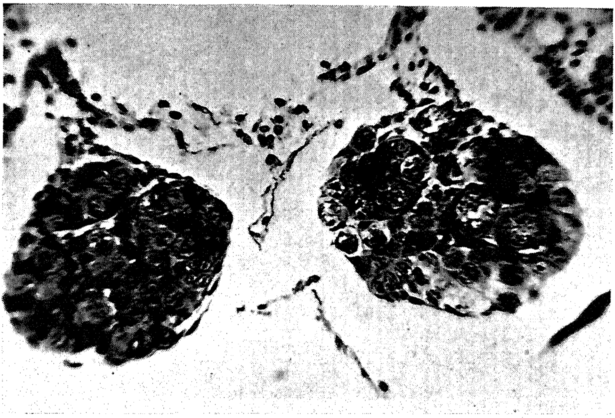

FIG. 2

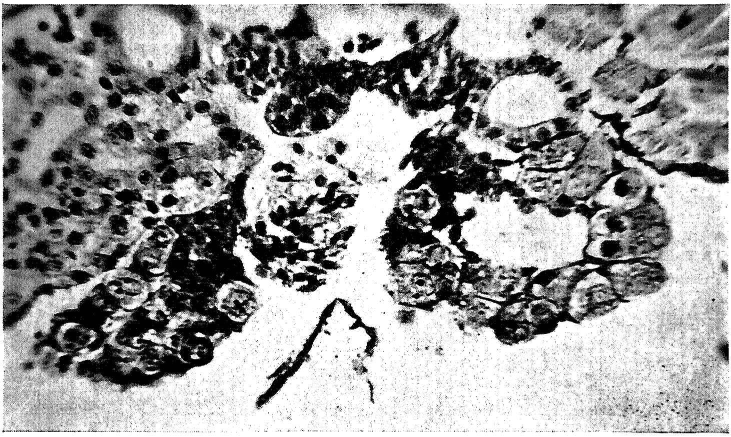

FIG. 3

HYPOGENITALISM IN *RANA CANTABRIGENSIS* *

TSO-HSIN CHENG

HYPOGENITALISM designates a condition of gonad underdevelopment. It has been contended that this abnormality is associated with, or rather is a result of, the process of sex reversal. Our present evidence, however, lends little support to this contention, but indicates that hypogenitalism and sex reversal are essentially two separate phenomena. Neither one of them, as shown by our data, is the cause or consequence of the other.

DESCRIPTION OF MATERIAL

A. Hypogenitalism in the adult wood-frog

Case 1. — This adult frog was caught near Ann Arbor, Michigan, and killed in Bouin's fixing fluid on October 13, 1928. It measures 35.5 mm. in body length and shows typical male external characters in the dark body coloration, the absence of dermal papillae, the convex condition of the webs of the hind-limbs and the presence of well-defined and pigmented finger-pads. The general build of the body indicates that it was a healthy, strong animal, though not especially robust.

The sex apparatus of this frog is purely male. There is no trace of Müllerian ducts nor of any ovarian tissue. The Wolffian ducts present the normal male pattern in having seminal vesicles below the level of the kidneys. The testes, however, are unusually small in all dimensions. The left gland measures 0.50 mm. in length by 0.55 mm. in width and 0.40 mm. in thickness,[1] the right one has a length of 0.55 mm., with a mean diameter of about 0.25 mm. (Pl. XLV, Fig. 1). Comparison of these testes with those of frogs of the same size and of the same season makes it obvious that their small size cannot be regarded as a normal individual variation, but is distinctly an abnormal feature.

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* Contribution from the Zoölogical Laboratory of the University of Michigan.

[1] All dimensions of the gonad are taken at maximum value, unless otherwise stated.

The surface of the abnormal testes is not smooth, but presents numerous minute concavities, some of which are so deep as to appear in the photograph like dark pits. The left testis is entirely devoid of any external pigmentation; the right testis, however, shows one distinct pigmented spot of comparatively large size and several smaller ones. The position which these gonads occupy is more caudal than usual. Vasa efferentia are absent as such and no trace of them can be found. The kidneys are normal. The fat-body is completely lacking on the right side; on the left it attains an unusually large size, consisting of two main parts, one above the other, both of which are massive with branches extending from their anterior, posterior and external borders. One may suppose that the upper part of the left fat-body was originally the right one transferred to the opposite side, but the morphological structure of the material affords no evidence for this.

Microscopically, the right gonad is found to consist of only a few spermatic tubules, most of which are much smaller than those in normal testes. The surface peritoneum shows distinct localized thickenings (Pl. XLV, Fig. 2). The tubules are filled compactly with germ cells and lack the normal central lumina. Spermatogenesis is in progress, as evidenced by the presence of numerous spermatocytes. Spermatids are few; spermatozoa are still fewer and are scattered about irregularly. In normal testes of this season, well-differentiated spermatozoa are numerous and grouped in characteristic bundles. The intratubular tissues of this atrophic testis are frequently clumped together and mixed into an agglomeration, which is in sharp contrast to the orderly segregation of germinal elements in normal tubules. The demarcation of the tubules is sometimes indistinct or absent, and the contents of two or more adjacent tubules appear to be massed together in disorder. Intertubular tissue is scanty, as in normal adult testes of this species.

The histological structure of the left gonad also reveals many signs of abnormality (Pl. XLV, Fig. 3). The seminiferous tubules are smaller than normal, and with rare exceptions, central lumina are entirely absent. In many tubules, the germ cells from the primitive spermatogonia to the mature spermatozoa are mixed together without any organization whatsoever. A few peripheral tubules are degenerating, and large dark rounded globules, apparently degenerate products of the germinal tissue, are occasionally encountered in different parts of the gonad. Only in one instance are the spermatozoa seen in bundle formation; elsewhere they show no such tendency. Intertubular tissue appears normal.

B. Hypogenitalism in wood-frog tadpoles

The materials used in this study have been described by the writer in the preceding paper (pp. 353–368). Among about three hundred tadpoles, there are found nine cases of intersexuality and five of hypogenitalism. Considering the number of larvae examined, these abnormalities must be regarded as quite rare.

Case 2. — A larva 26 days old,[2] with a total length of 19 mm. The right gonad measures 500 × 64 × 40 micra; the left one 500 × 88 × 56 micra. Neither gonad shows any morphological indication of sex differentiation. A simple surface peritoneum incloses the so-called primary genital cavity, which is filled with loose embryonic tissue. Clusters of rete cords project into the gonads and occupy their entire interior at definite intervals. The germinal elements are very scanty. In the right gonad, there are about ten gonial cells, two of which are in mitosis. The left gonad contains only two primordial germ cells which still retain granules of yolk material. In normal gonads of larvae of the same age, germ cells are numerous, generally one or two hundred, and are aggregated peripherally, forming, with the peritoneal membrane and some mesodermal elements, a primitive germinal epithelium.

Case 3 (Pl. XLVI, Fig. 1). — A larva 61 days old, with a total length of 33.5 mm. The right gonad measures 350 × 160 × 150 micra and is structurally a normal testis. The left gonad, measuring 520 × 120 × 80 micra, has a definite testicular appearance, and is densely packed with mesenchymatic tissue, imbedded in which only three or four spermatogonia have been detected. Normal gonads of this age are well-developed testes and ovaries and contain numerous sex cells. The left fat-body of this specimen is normal, but the right one is very small.

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[2] Age of tadpoles is calculated from the time of egg-laying.

Case 4 (Pl. XLVI, Fig. 2). — A larva 85 days old, with a body length of 36 mm. and hind-limbs about 10 mm. long. The right gonad measures 280 × 150 × 60 micra; the left one 250 × 130 × 70 micra. The former gland appears like an abortive testis in being abnormally small and in containing a relatively large amount of mesodermal elements. The latter gland is practically sterile, with only one diminutive gonium and two or three doubtful, probably degenerating, germ cells imbedded in disorganized masses of mesenchyme. Both fat-bodies attain an exceedingly large size. In comparison with them, the gonads appear as mere vestigial structures.

Case 5 (Pl. XLVI, Fig. 3). — A larva 91 days old. It measures 14 mm. in body length, has well-developed fore- and hind-limbs, and a tiny stump of the tail. The right genital gland measures 700 × 120 × 100 micra and is a sterile gonad. A central gonadic cavity is well defined throughout, lined by a distinct mesothelium. The space between this inner mesothelium and the surface peritoneum is filled with loose connective tissue. A fairly large, cell-like body, containing numerous intensely staining granules, is present. It is unquestionably a degenerating structure, but its cellular nature is problematical.

The left gonad is a rudimentary ovary, measuring 550 × 270 × 110 micra. It contains distinct ovarial sacs, surrounding which is a thin peripheral ring of oögonia and young oöcytes, comparable to the germinal epithelium in an early stage of ovary development. Large auxocytes are few and often project into the central cavity. Some germ cells develop large, rounded, intensely basophilic bodies in the nucleus, which are undoubtedly pathological features. The side-wall of the ovarial sacs is thin and the interstitial tissue scanty.

The fat-bodies, especially the right one, are larger than in normal frogs of this age. On the lateral side of the kidneys, there is developed a strip of thickened peritoneum, which is the *Anlage* of the future oviduct.

Case 6. — A metamorphosing tadpole 113 days old, measuring 14 mm. in body length. The right germ gland measures 500 × 360 × 240 micra and is a testis of normal size. Spermatogonial cells are conspicuous by their abundance and crowded condition. Rete-cord cells are relatively scanty; otherwise, the gonad shows no deviation from the normal testicular structure. The left gonad is an attenuated gland, measuring only 200 × 200 × 48 micra. The whole organ is compactly filled with mesenchymatous cells. There is no visible trace whatsoever of any germinal tissue. Both fat-bodies are normal.

REVIEW OF THE RECORDED CASES OF HYPOGENITALISM IN FROGS

Marshall (1884) presented the first two specimens of gonadic atrophy in *Rana temporaria*, the first a male frog in which the right testis is almost completely absent, the left one of unusual size, and the Müllerian ducts larger than usual and convoluted; the second, perhaps an aborted male with well-developed Müllerian ducts and rudimentary gonads represented by a pair of small oval masses of fat.

Pedaschenko (1890) found the gonads and the accessory sex organs all lacking in an externally normal male of *Rana temporaria*. The Müllerian ducts were well developed and the fat-bodies were extremely large.

Loisel (1901) recorded a female frog (*Rana temporaria*) exhibiting male secondary sex characters. Two oviducts were present and the ovaries were very rudimentary: the right ovary was practically lacking; the left one was small and, according to the author, was invaded by a pigmented body which ramified in its interior.

Nussbaum (1906 a) described in *Rana fusca* testes of unequal sizes and atrophied testes in starved frogs. In 1912, he reported two abnormal males of the same species. One presented "einen Zwerghoden rechts, bis zum verschwinden klein gegen den linken Hoden," and the other possessed only one testis, with small seminal vesicles as well as Müllerian ducts on both sides.

Hooker (1912) discovered a male specimen of *Rana fusca,* the left gonad of which was missing and the right testis slightly hypertrophied. Small Müllerian ducts were present.

Patzelt (1918) observed rudimentary ovaries and immature oviducts in an adult female of *Rana esculenta.* He has also described (1923) testicular atrophy in two males of the same species.

Bhattacharya and Das (1920) described a male frog of *Rana tigrina,* in which a pair of moderately developed Müllerian ducts were present, and in which the right testis was very small and degenerate, without any associated vasa efferentia.

Lloyd (1921) observed a specimen of *Rana temporaria* possessing a greatly hypertrophied testis on the left side and showing no trace of a testis on the right.

Witschi (1921) noticed in a vigorous adult grass-frog a hypertrophied left testis and an atrophic right testis. The same author (1924) found three metamorphosing tadpoles, in which either one or the other of the two gonads was rudimentary. The rudimentary gonads were associated with somatic deformities as well as with an alleged sex transformation in the female-male direction.

Dornesco (1926, 1927) reported in *Rana esculenta* two cases of congenital monorchidism, both of which showed the total absence of a left testis.

Dubois and Ponse (1927) noted five specimens of hypogenitalism among the water-frogs (*Rana esculenta*), only two of which were described. The frogs were female in external appearance, and possessed moderately developed oviducts and rudimentary ovaries with signs of degeneration.

So far, no case of hypergenitalism has been recorded in early larval specimens, and indeed, little, if anything, has been known about the embryonic history of underdeveloped gonads.

ORIGIN OF HYPOGENITALISM

Various hypotheses have been advanced to explain hypogenitalism in frogs. Some of them are purely conjectural, and none of them appears to be supported by substantial and conclusive evidence. Marshall (1884) thought gonadic atrophy was due to a further extension backward of the process of fatty degeneration, which had resulted in conversion of the most anterior part of the genital ridge into the fat-body. Loisel (1901) held that a certain pigmented body was the responsible factor for ovarian atrophy, and implied the possibility that the pigmented body might be parasitic in nature. Nussbaum (1906 a, b) concluded from a series of observations and experiments that long starvation prohibited the normal formation and development of the germinal elements in frogs' testes. Contrary to this conclusion, Patzelt (1918, p. 275) found, in a frog starved for about two years, well-developed testes normal in all respects. According to Patzelt, underdeveloped gonads "sind grossenteils auf einer jugendlichen Entwicklungsstufe stehen geblieben und wurden teilweise durch Fettgewebe vertreten." Bhattacharya and Das (1920) suggested that testicular atrophy is due to a tendency of the gonads to degenerate after reaching a certain stage of development. Such a tendency may be of a similar nature to "Altinvolution" in Patzelt's terminology. Hooker (1912) and Crew (1921) listed cases of gonad absence among their sex-reversal types. Witschi (1921) argued that "Zwerghoden" was merely the remains of a degenerated ovary in the process of sex reversal. Dubois and Ponse (1927) were also inclined to regard their cases of hypogenitalism as a question of "stades intersexués comparables aux 'intermédiaires' de Hertwig et Kuschakewitsch."

In our material, there is little evidence that atrophied gonads are the result of a process of fatty degeneration. The fat-body in most cases is normal, or actually smaller than normal, and may even be lacking altogether (Case 1, right gonad). It cannot be denied that under certain circumstances rudimentary conditions of the gonads may lead to the enlargement of the fat-bodies (Case 4, 5 and 1, left gonad), which is most probably the result and not the cause of the gonadic atrophy. Pigmentation is absent in our abnormal gonads, except in the adult specimen. In it the pigments are evidently products of tissue degeneration and not parasitic organisms. Our frogs are all externally normal and healthy, which is convincing proof that starvation is not a causative factor here. As already pointed out in a preceding section of this paper, our cases of hypogenitalism have no relation to sex reversal.

In the adult specimen, all sex organs and characters are typically male, exhibiting no female feature whatsoever. In cases 4, 5 and 6, in which only one gonad can be accurately sexed, there is no evidence that the other gonad is of the opposite sex or is intersexual. In case 3, both gonads are of the same sex and differ only in the degree of development. All available evidence appears, thus, to be in perfect agreement with our contention that hypogenitalism is primarily an abnormality by itself and not connected with the problem of sex differentiation. We do not imply, however, that sex reversal may not occasionally be capable of inducing gonadic deficiency, although this is not so in the cases we have so far encountered.

Without further discussion of the various views regarding the genesis of hypogenitalism in frogs, our present data seem adequate for a tentative postulate of two factors, which, in our opinion, will explain a large number of the facts recorded above.

First, the primordial germ cells may fail to migrate to the gonadic region. In *Rana cantabrigensis*, as in other species of frogs, the primordial germ cells, when first found, are large yolk-laden cells included in a ridge of entoderm just dorsal to the archenteron. As development proceeds, they become separated from the entodermal cells and eventually migrate to their definitive position, where gonads are to be formed. Failure of the germ cells to do so would result, as shown by the work of Reagan (1916) and Humphrey (1927), in a more or less complete suppression of the genital gland or in the formation of a sterile gonad. In the light of this basic conception, it becomes apparent that the abnormal absence of germ cells in the gonad of one or the other side, as in cases 5 and 6, may be due to the failure on the part of the germ cells to reach the gonad region of that particular side. This may occur in either sex and in either or, rarely, both sides.

Numerical studies of the primordial germ cells (Beard, 1902; Allen, 1907; Firket, 1914; Swift, 1915; and others) appear to show that for a normal embryonic gonad it would require at the very outset a certain minimum number of germ cells. An insufficiency of the primordial germ cells would induce some kind of gonadic deficiency. This seems to hold true in cases 2, 3, left gonad, and probably in other similar cases.

Secondly, the germ cells may fail to develop normally. The occurrence of degenerating sex cells in cases 1, 4, left gonad, and 5 suggests an abnormality of the germ-cell development. Undoubtedly, germ cells under certain circumstances may be retarded or delayed in growth and differentiation; or they may actually be prevented from undergoing a normal course by some disturbances during critical periods of gonadic development. This disturbance, as evidenced by our data, is of a specific nature, and its effect is definite and localized. Kidneys, mesonephric ducts and accessory sex organs (seminal vesicles in case 1 and oviducts in case 6) may develop in a normal fashion, despite the abnormal condition of the gonads.

These two factors are by no means the initial causes, but are themselves mere symptoms of a more fundamental derangement of the germ-plasm. This derangement, in turn, may be occasioned by genetical incompatibility of a certain nature, as shown by the hybridization results of Smith and Haig Thomas (1913), Whitman (1919), Harrison (1920), Riddle (1925) and others; or by any adverse environmental condition or agency, be it internal or external, metabolic, hormonic or otherwise. The developmental processes of the gonads and the germ cells apparently can be modified by various experimental means, such as late fertilization (Kuschakewitsch, 1910), inanition (Swingle, 1918), altered oxygen pressures and low temperatures (Riddle, 1925), and the like. Witschi (1924) has presented data which show that overripeness of eggs may cause, among other abnormalities, underdeveloped gonads as well as sex transformation. In his recent studies (1929), high temperature is shown to be capable of inducing degenerative changes in the germ cells of both sexes, and also reduction of the size of the gonads. Further experimentation along genetic and embryological lines may reveal the mechanism which is effective, and the condition involved, in the genesis of hypogenitalism.

I wish to express my sincere gratitude to Professor Peter Okkelberg for the kindly and inspiring interest he has shown in my work.

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EXPLANATION OF PLATES XLV–XLVI

PLATE XLV

FIG. 1. Photograph showing the abnormal testes *in situ*. Magnification approximately × 10

FIG. 2. A transection of the right testis, showing tissue hyperplasia along the gonad peritoneum. Magnification approximately × 125

FIG. 3. A transection of the left testis. Note the disorganization of germinal cells in some of the tubules. A few degenerating peripheral tubules are seen as sclerotic masses of dark bodies, with the general outline of the tubules still recognizable. Magnification approximately × 125

PLATE XLVI

FIG. 1. A transection through the anterior third of the right testis and the middle portion of the left (case 3). Note abundance of somatic elements in the latter gonad. Magnification approximately × 125

FIG. 2. A transection of the atrophic gonads of case 4. Under higher magnification many sex cells can be seen in the right gland. Magnification approximately × 100

FIG. 3. A transection of the urogenital organs of the larva in case 5. The embryonic oviducts are present on the lateral margin of both kidneys. Note the complete absence of germinal substance in the left gonad, which has a persistent secondary gonad cavity — a characteristic feature of the ovary. Magnification approximately × 50

PLATE XLV

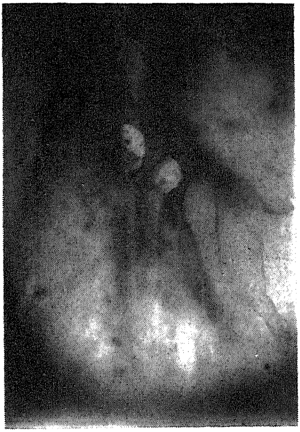

FIG. 1

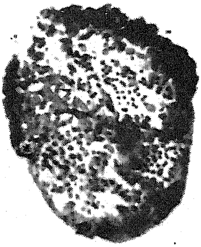

FIG. 2

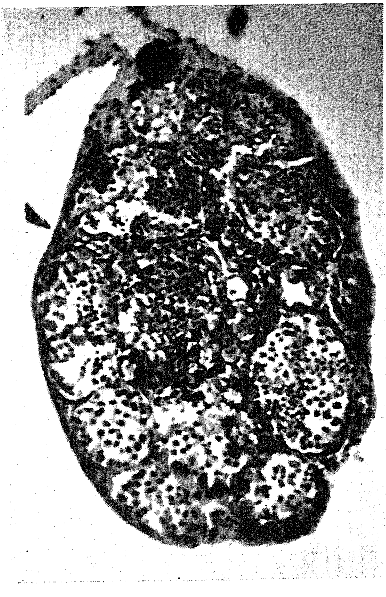

FIG. 3

PLATE XLVI

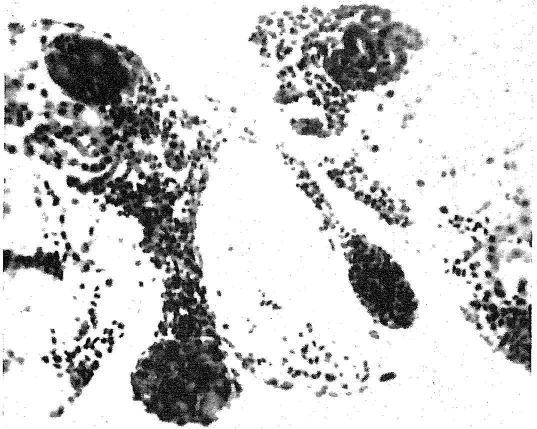

FIG. 1

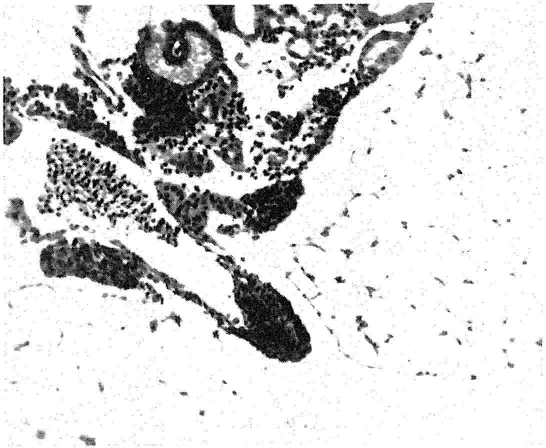

FIG. 2

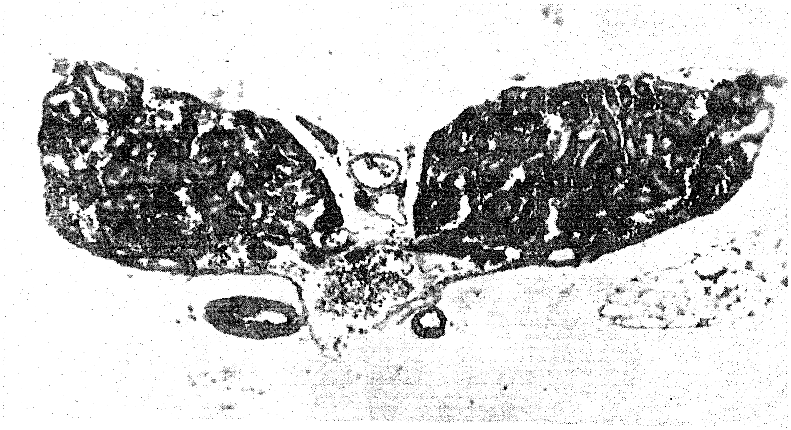

FIG. 3

THE PHYLLOPODA OF MICHIGAN *

EDWIN P. CREASER

IN PUBLISHED accounts but a single species of Phyllopoda has been recorded from Michigan. Pearse (1910, p. 69) lists *Eubranchipus vernalis* from near Ann Arbor. Two other species, *Eubranchipus bundyi* and *Lynceus brachyurus brachyurus*, are now known to occur in this state. Some ecological observations are reported here, since the environmental relationships of the various members of Phyllopoda are, as yet, poorly known. Identification of the Michigan species may be made by means of the key and figures contained in this paper.

Ecologists have continually referred the fairy shrimps of the genus *Eubranchipus* to the temporary pond association. These animals are often found in ponds near Ann Arbor which dry up only occasionally during the summer. Certain parts, however, are very shallow and become dry as the water level lowers with the advance of the season. These parts probably supply the fairy shrimps, since the Hays (1889, p. 92) have shown that the eggs of *Eubranchipus* must be dried before development occurs.

Ponds that are closely adjacent often contain a vastly different population of fairy shrimps as regards number of individuals. Near Alma, Michigan, there are two ponds no more than one hundred yards apart, one on the edge of a hardwood area, the other in the middle. In the latter, *Eubranchipus bundyi* (Figs. 10, 11, 17) were present in 1928 in vast numbers, but in the former the population was very sparse, perhaps on account of predacious enemies. This pond on the edge of the woods contained many spring-peepers, *Hyla crucifer*, and many amphibian eggs were also found in the water. Fishes and frogs will consume fairy shrimps in laboratory aquaria, but recorded observations of their feeding on these animals under natural conditions are not available. It is probable, however, that amphibians are potent factors in controlling the numbers of *Eubranchipus.*

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* Contribution from the University of Michigan Biological Station and from the Zoölogical Laboratory of the University of Michigan.

My observations on the types of habitat of these animals do not agree with those of Shelford (1913, p. 179), who says that *Eubranchipus* (species not stated) is found only in grassy ponds. He suggests that the ponds in forests probably do not dry sufficiently in summer. In Michigan, however, I have found the species of this genus recorded in the present paper to be most abundant in woodland pools.

Color differences were noted between the specimens of the same species of *Eubranchipus* in woodland ponds and those in ponds located more in the open. Fairy shrimps raised in the laboratory do not exhibit the delicate tints of color displayed by the animals in their natural habitat.

O. P. and W. P. Hay (1889, p. 92) have shown that it is possible to raise *Eubranchipus bundyi* (*Branchipus gelidus*) in the laboratory by placing females with ripe eggs in an aquarium. Subsequent to the death of the animals, they dried the mud, which they later replaced in the water. After a lapse of about two weeks the animals again appeared. Freezing of the eggs was not necessary. *Eubranchipus vernalis* (Figs. 8–9) can also be raised in the laboratory, since I obtained two males from mud containing eggs, taken from a pond near Ann Arbor late in November, 1928. The water in this experiment was not aërated and became bog-stained before the animals appeared.

Fairy shrimps have been known to occur during warm periods in winter, but usually do not attain sexual maturity before being killed by the onset of inclement weather. Shelford (1913, p. 179) records Dr. Child's observation of their occurrence in the early part of the winter near Chicago, Illinois. The renewal of cold weather killed the animals before they had attained sexual maturity and for several years thereafter they were very scarce in that region. The two species of *Eubranchipus* occur normally in Michigan as adults from April to May, according to the season.

Structures thought to be parasitic cysts have been observed in *Eubranchipus vernalis.* Gissler (1881, pp. 101–102) mentions their occurrence in this fairy shrimp from the eastern part of the United States. He fed infected animals to frogs, but found no traces of infection upon post-mortem examination. Fairy shrimps from Oregon also have structures which appear to be cysts of trematode cercariae. It is entirely possible that Michigan species will be found infected with parasites.

Some of the other associates of the species of *Eubranchipus* in Michigan are as folows: — amphibians: *Rana pipiens, Rana cantabrigensis, Hyla crucifer, Ambystoma maculatum, Ambystoma tigrinum;* molluscs: *Musculium securis, Lymnaea obrussa;* cladocerans: *Daphnia pulex;* amphipods: *Eucrangonyx gracilis;* isopods: *Asellus communis;* and insects of the following genera: *Gerris, Corixa, Gyrinus, Haliplus, Bidessus* and *Hydroporus.*

Lynceus brachyurus brachyurus, a phyllopod sometimes called the clam shrimp, occurs in ponds which are usually permanent. This is accounted for, no doubt, by the fact that they live somewhat longer than the other species in the state. I have taken them in July, one month and a half after the disappearance of *Eubranchipus.* Johansen (1923, p. 2) has taken these clam shrimps in company with the fairy shrimps, *Eubranchipus bundyi* ("*gelidus*"), in Ontario. In Michigan they sometimes occur with the two species of *Eubranchipus* in ponds, sections of which become dry during the summer.

Lynceus (Figs. 12–16) was found in great numbers on July 8, 1928, at Penny Lake, Cheboygan Co., Michigan. This small lake is surrounded by burnt-over swampy land; is in no place more than four feet deep; and contains an abundance of sedges and water lilies. Chemical data were obtained for this lake by E. P. Cheatum on July 8, 1928. His results are as follows: pH 6.1, dissolved oxygen 2.12 c. c. per l., carbonates 0.0 p.p.m., bicarbonates 18 p.p.m., free carbon dioxide 11 p.p.m., temperature 22° C. At the time these determinations were made, the animals were sexually mature. A month later all the individuals had disappeared. Chemical data secured by Mr. Cheatum on August 7, 1928, were: pH 5.4, free carbon dioxide 14 p.p.m., dissolved oxygen 2.65 c. c. per l., carbonates 0.0 p.p.m., bicarbonates 5.0 p.p.m., temperature 23° C.

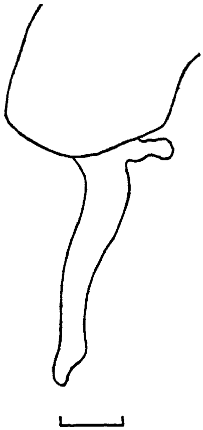

FIG. 8. Clasping antenna of male *Eubranchipus vernalis*

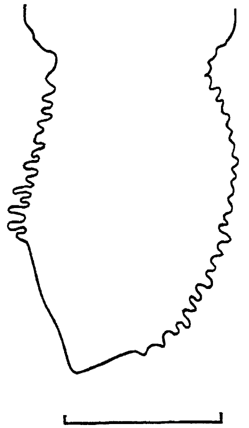

FIG. 9. Frontal appendage of male *Eubranchipus vernalis*

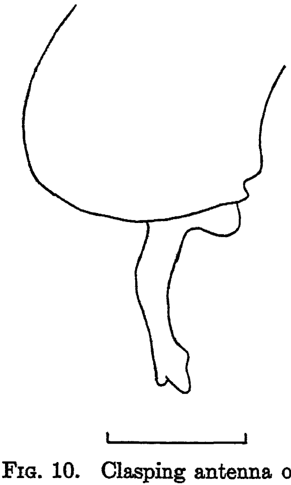

FIG. 10. Clasping antenna of male *Eubranchipus bundyi*

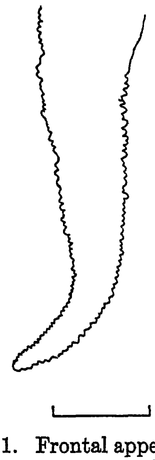

FIG. 11. Frontal appendage of male *Eubranchipus bundyi*

FIGS. 8–11. Features used in the identification of the Michigan species of *Eubranchipus*. The scale for each figure is equal to one millimeter

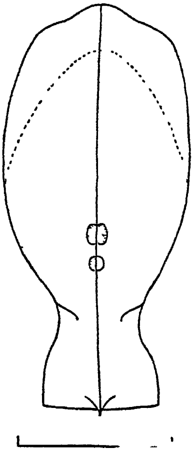

FIG. 12. Frontal view of head of male *Lynceus b. brachyurus*

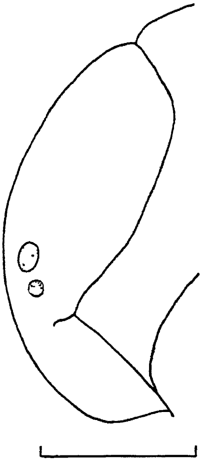

FIG. 13. Lateral view of head of male *Lynceus b. brachyurus*

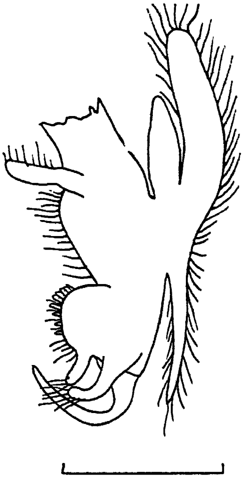

FIG. 14. First swimming appendage of male *Lynceus b. brachyurus*

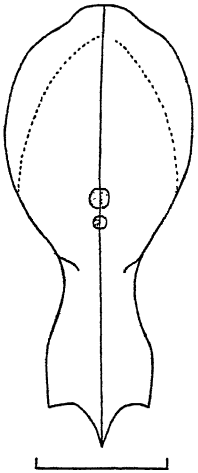

FIG. 15. Frontal view of head of female *Lynceus b. brachyurus*

FIGS. 12–15. Some of the features useful in identification of *Lynceus b. brachyurus*. The scale for each figure is equal to one millimeter

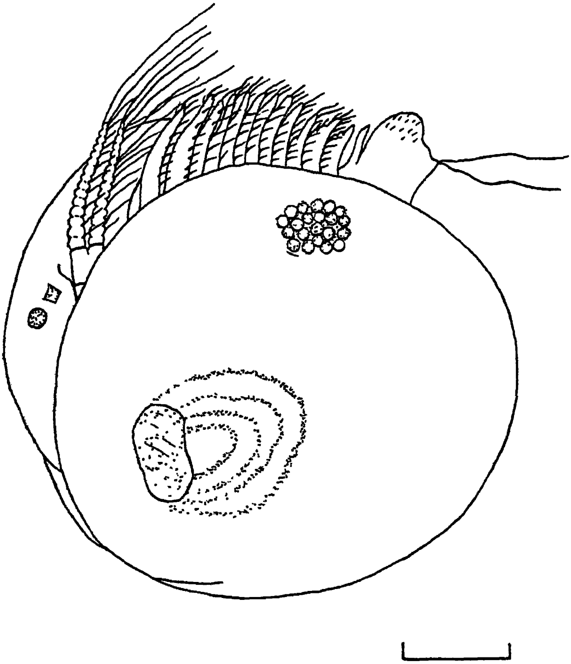

FIG. 16. Lateral view of *Lynceus b. brachyurus*

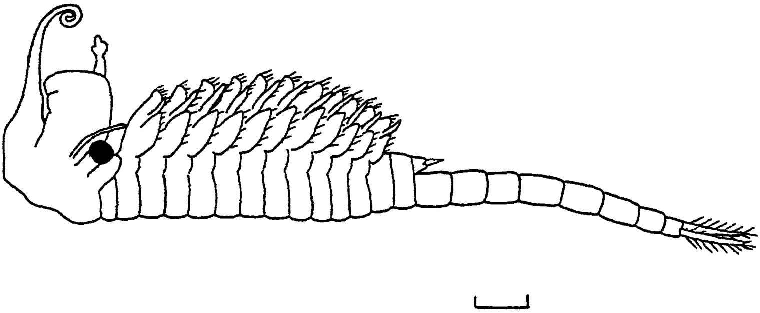

FIG. 17. Lateral view of *Eubranchipus bundyi*

FIGS. 16–17. Drawings of entire animals, illustrating some of the generic differences. The scale for each figure is equal to one millimeter

Specimens of *Lynceus* taken from Penny Lake had profuse growths of the ciliate protozoan *Epistylis* upon the shells and even upon the rostrum. These Phyllopoda are yellow-white or amber. The eggs of this species can be plainly seen beneath the posterior part of the shell. As many as two hundred are often found. A sort of brood chamber is formed by the curling of the greatly elongated flabellum of the ninth and tenth swimming appendages. The eggs adhere closely together and the ones adjacent to the flabellum are attached to that organ by setae.

DISTRIBUTION

Known localities for the three species in Michigan are:

Lynceus brachyurus brachyurus: Ann Arbor, Alma and Penny Lake, Cheboygan County.

Eubranchipus vernalis: two localities near Ann Arbor in Washtenaw County.

Eubranchipus bundyi: Ann Arbor, Alma, Ypsilanti, and South Lyon.

KEY TO THE MICHIGAN SPECIES OF PHYLLOPODA

1 a. Body not inclosed in a bivalve carapace. Eyes pedunculate. Head of male bearing a single frontal appendage on the base of each clasping antenna. Frontal appendage absent in the female. Eleven pairs of swimming feet. First pair without clasping devices at the apex. Second antenna modified for clasping and composed of two segments. Genus *Eubranchipus*

- 2 a. Frontal appendage on the base of the male clasping antenna long; three times the length of the basal segment. Body segments nine and ten in the female produced into protuberances directed posteriorly. . . . . *Eubranchipus bundyi* Forbes [1]
- 2 b. Frontal appendage on the base of the male clasping antenna short; not extending beyond the basal segment. Female body segments not modified. . . . . . *Eubranchipus vernalis* (Verrill)

1 b. Body inclosed in a plain bivalve carapace. Eyes not pedunculate. Head beak-shaped, broad in the male and acuminate in the female. Ten pairs of swimming feet in the male, twelve in the female. First swimming appendage of male with apical clasping hook. Dorsal antenna composed of a base and two flagella, not modified for clasping, and with more than 15 segments. . . . . Genus *Lynceus*

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[1] I consider *Eubranchipus gelidus* (Hay) a synonym of this species.

3a. Rostrum of female acutely triangular. Subanal lamina entire, rounded distally. Apical segment of male first swimming appendage with two club-like protuberances (endites) nearly equal in size. Hook (endite 6) on this segment uniformly tapering. Inner side of apical clasping device in the male not completely setose above the smaller club (endite 4). *Lynceus b. brachyurus* Müller

UNIVERSITY OF MICHIGAN

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ORNITHOLOGY AND FOREST ENTOMOLOGY *

SAMUEL A. GRAHAM

EVERY biologist is ready to agree that birds are of value in reducing the abundance of noxious insects. The works of Forbes, McAtee and many others, not to mention the results of our personal observations, are too conclusive to leave room for argument. But when we are asked to state in specific terms exactly how important is the service of birds as insect destroyers we must, as a rule, either sidestep the issue or plead ignorance. We know what birds eat, but relatively little of how much of the various kinds of food they require. Neither do we know in quantitative terms the effect of the normal bird population upon insect life. From the viewpoint of forest entomology these questions are important and must be answered. Quantitative studies of bird foods by ornithologists would be of inestimable value to the forest entomologist.

In the study of forest defoliators the need for more information concerning the food of birds is especially apparent. During the past few years the author has carried on a series of experiments to determine the effect of various factors of environmental resistance upon the larch sawfly, *Lygeonematus ericsonii.* In these investigations the influence of birds was studied to some extent. Some of the observations made during these studies are reported here partly because they may be of general interest and partly because they may serve to indicate some of the contact points lying between ornithology and forest entomology, contact points that should receive attention.

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* The data upon which this paper is based were collected in the course of studies conducted coöperatively by the Bureau of Entomology, U. S. Dept. Agric., the University of Minnesota, and the University of Michigan, at the field station of the University of Minnesota Forest School at Itasca Park.

THE BIRD CENSUS

In order to arrive at an evaluation of the effect of birds as a factor of environmental resistance, it is necessary first of all to know what birds are present in an area under investigation and the relative abundance of the various species or groups of species. During the nesting season of 1928 a census was made of the bird inhabitants in the vicinity of our larch sawfly sample plots in Itasca Park, Minnesota. Although this census was not as extensive or complete as one would like to see it, nevertheless the results are significant.

An attempt was made to determine by actual count the number of nesting pairs on one acre sample plots. We found that this could be done with satisfaction only in the very early morning before the birds moved from their roosts. The number of males singing or calling at that time was taken as an indication of the number of pairs. This method required that the observer be at his station before daylight, so that he would be ready to catch the first notes of each male. By the time the sun rose the birds were usually moving about, so that it was impossible to count them with satisfactory accuracy. Thus observations could be made at only one station each morning, with the result that the number of observation points was necessarily limited.

In addition to recording the number of pairs on each sample acre examined, the birds heard or observed in the vicinity of the plots were also recorded, thus supplementing our rather limited quantitative records with more extensive qualitative observations.

The observation stations, as we have previously stated, were located in the vicinity of our larch sawfly experimental plots. Some were actually on these plots, whereas others were located in adjoining areas. The location of the stations is indicated in Figure 18. In this way the study was not limited to the birds of the tamarack swamp type, but included those of other forest types. For instance, plots 1, 3 and 5 were in the tamarack swamp, whereas number 2 was in a mixed hardwood forest at the edge of the swamp, number 4 in a forest of second-growth aspen and birch with occasional

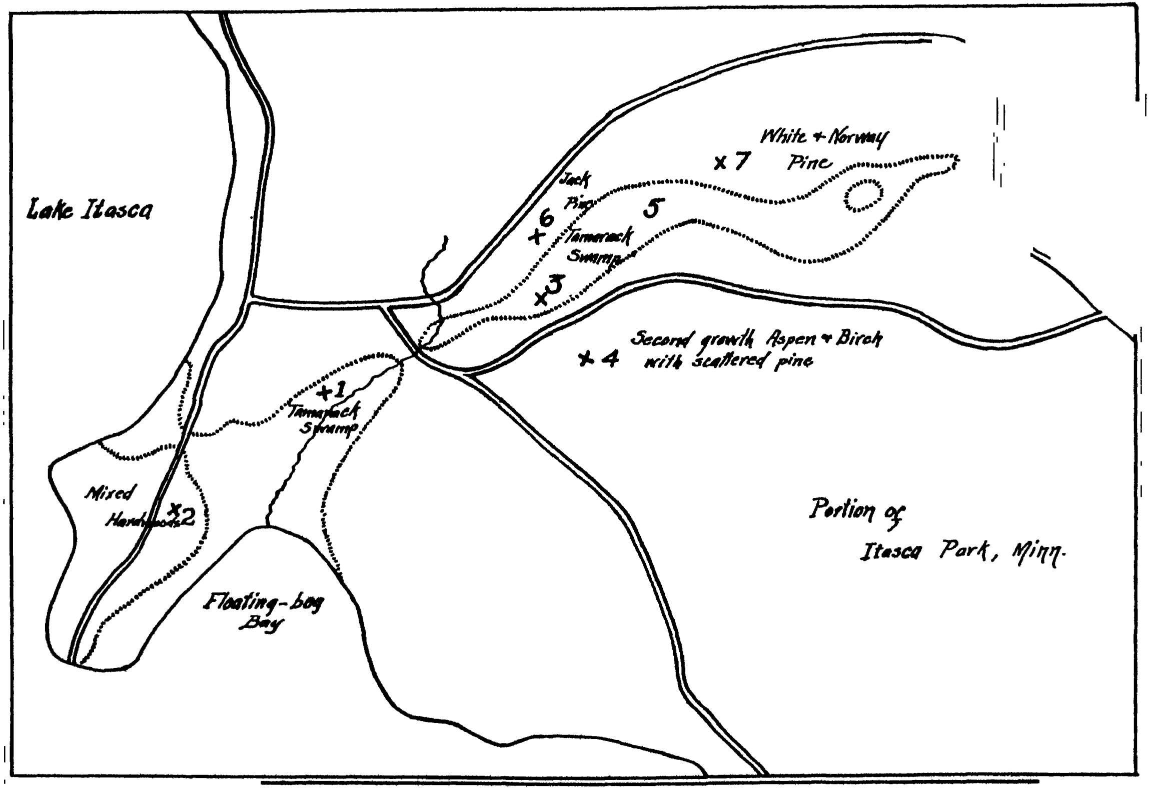
Lake Itasca
White + Norway Pine
× 7
5
Jack Pine
× 6
Tamarack Swamp
× 3
Second growth Aspen + Birch with scattered pine
× 4
× 1
Tamarack Swamp
Mixed Hardwoods
× 2
Floating-bog Bay
Portion of Itasca Park, Minn.

FIG. 18

large white and Norway pines, number 6 in a jack pine forest, and number 7 in a virgin forest of white and Norway pine. These seven plots were all in or near the same swamp, known as Floating Bog Swamp, and were from one eighth to one half mile apart. Other observations were made in other swamps, but the plots listed above represent the most complete series made.

The records made on these plots indicate clearly that during the nesting season the bird population is not concentrated in certain areas, but is relatively evenly distributed in various forest types in the same general locality. On each of five of the seven plots there were four nesting pairs, on one there were five pairs,[1] and on one there were six pairs.

Although the number of pairs per acre in and around the swamp was fairly constant, the species present in each type varied, as one might expect. Table I illustrates the distribution of species or groups. Owing to the difficulty of identifying the warblers specifically with the trees in full foliage, the members of this family have been grouped together. Some representative of this group was found on every plot except one and a nest was located just off that plot.

Although the number of pairs per acre in the swamp is very little, if any, greater than in the surrounding forest, from the foregoing table it appears that there is a greater variety of species in the swamp than on the adjacent higher ground. This condition would naturally follow from the fact that there is a greater variety of plant growth and a consequent greater variety of food in the swamp type than in most other types. It would be extremely interesting to know whether or not a similar distribution of nesting birds exists over more extensive areas.

To judge from the birds heard and observed in the near vicinity of the plots, it seems practically certain that other combinations of species would doubtless be found within a short distance of the points where observations were made.

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[1] The fifth record on this plot is questionable. A male tree-sparrow was observed on the plot at daybreak, but no nest was found. He did not sing and may have been a single male wandering beyond the usual breeding range of the species, in which case there were only four pairs on this plot.

TABLE I

Distribution of Birds in Various Forest Types

The plus sign (+) indicates the presence of the species on at least one plot in the type indicated.

Species	Swamp	Mixed hardwoods	Second-growth aspen	Jack pine	White and Norway pine
Warblers	+	+	+	+	+
Veery	+	−	+	−	+
Olive-backed thrush	+	−	−	−	−
Robin	−	+	−	−	−
Tree-sparrow	?	−	−	−	−
White-throated sparrow	+	−	−	−	−
Song sparrow	+	−	−	−	−
Traill's flycatcher	+	−	−	−	−
Wood pewee	−	−	+	−	−
Black-capped chickadee	+	+	−	−	−
Red-eyed vireo	−	−	−	+	+
Warbling vireo	−	−	−	+	+
Ovenbird	−	−	+	+	+
White-breasted nuthatch	+	−	−	−	−

Some of the species heard or observed near but not on the observation plots were:

Arctic three-toed woodpecker
Barred owl
Blue-headed vireo
Blue jay
Chipping sparrow
Crested flycatcher
Crow
Downy woodpecker
Great horned owl
Hairy woodpecker
Hudsonian chickadee
Kingbird
Least flycatcher
Maryland yellowthroat
Mourning dove
Night hawk
Phoebe
Pileated woodpecker
Red-winged blackbird
Scarlet tanager

Any bird in this list might easily have been on one of the plots. From the results of this census, it seems probable, however, that the concentration of pairs per acre would remain relatively constant in the immediate vicinity of the swamp studied, even though the species on different plots would not be the same. Perhaps the concentration of four pairs plus per acre represents the point of population saturation for the vicinity of Floating Bog Swamp. In another locality, however, under other conditions of food and shelter, the population per acre would, in all probability, be different.

BIRDS THAT FEED ON THE SAWFLY LARVAE

Now that we know the species of birds living in or near the tamarack forests attacked by the larch sawfly, we should next know which of these species feed upon the insect. We can, for all practical purposes, rule out the flycatchers, the owls, and the woodpeckers. None of these would be likely to feed on the larch sawfly larvae to any great extent. The other species are all distinct possibilities and it is probable that all of them may at times eat these larvae. By no means were they observed to do so, however. Most of the birds relied upon other kinds of insect food even though the sawfly was in abundance near their nests.

Certain species, however, did feed upon the sawfly larvae. For instance, the white-throated sparrow was seen repeatedly feeding on them. Less frequently the Maryland yellowthroat was seen doing likewise. The chipping sparrow appeared to feed freely on the larvae on some occasions whereas at other times it paid no attention to this easily accessible food-supply. Another bird that was observed to eat the sawfly larvae was the cedar waxwing. In one instance a blackcapped chickadee was seen to eat the larvae. Doubtless other birds may have fed upon them, but through five seasons of general observation no others have actually been observed in the act of picking them from the trees.

QUANTITATIVE EFFECTS OF BIRDS UPON THE SAWFLY LARVAE

In order to determine the effect of birds and other factors of environmental resistance upon the larvae of the larch sawfly, a series of experiments under natural conditions was outlined and carried through to completion during the summer of 1928.

The procedure in these experiments was as follows: On tamarack trees growing under natural conditions tips in which sawfly eggs had been deposited were tagged for observation. The number of eggs in each tip marked varied from 10 to over 100. The larvae of the larch sawfly are gregarious and sedentary in their habits. They feed in groups and move from branch to branch only under the pressure of food scarcity. These habits made it possible to follow each group of larvae that hatched from eggs in the tagged tips through their entire developmental period without caging them. Every other day the larvae in each group were counted carefully and the cause of any reduction in numbers was sought.

These observations were carried on at three different stations. The first was located in a group of planted tamaracks growing on high ground near the laboratory, the second in Floating Bog Swamp, and the third in a swamp that we shall call Iron Spring Swamp. At station 1 twenty groups of larvae were under observation; at stations 2 and 3 there were fifteen and ten groups, respectively. The groups of larvae in each series were distributed over a number of trees at each station so as to obviate the danger of complete destruction of an entire set during a single foray of some insectivorous animal.

When this experiment was started it was thought that a large proportion of the larvae would be found and eaten by birds. Such was apparently not the case, however. In series number 1 only one of twenty groups of larvae was destroyed. This group of twenty-four larvae was found by a chipping sparrow which had a nest near by and every larva was eaten. Other groups not far away remained untouched. In series number 2 three groups, containing at the time five, ten and four larvae, were probably eaten by birds, whereas in series 3 there was no evidence that birds found any of the larvae.

These data indicate that under the conditions existing, birds were a relatively unimportant factor of environmental resistance, so far as the larch sawfly larvae were concerned.

In view of these findings we might logically ask what is the reason that birds are not more effective enemies of this insect than they are. Are we to assume that they are no more effective in reducing the numbers of other insect species?

The answer to the first question appears to be simple. The eggs of the sawfly are deposited in the slender green tips of the tamarack trees. The larvae after hatching feed far out on the slender flexible tips. When all the foliage on one twig has been eaten, they move out to the extreme end of an adjoining twig to continue their feeding. It is not until a branch has been stripped of the foliage on the tips that the larvae are forced to feed on the larger twigs.

TABLE II

EFFECT OF BIRDS ON THE LARCH SAWFLY POPULATION

Series	Groups eaten by birds		Original number of Larvae	Larvae eaten by birds	
	Number	Percentage		Number	Percentage
1	1	5.0	833	24	0.3
2	3	20.0	238	19	8.0
3	0	0.0	497	0	0.0

In watching the action of birds in tamarack trees it has been obvious that they do not like to venture too far out on the slender twigs. Even small birds, like the chickadee or chipping sparrow, appear to prefer the more substantial twigs and branches. Thus it appears to be the exception rather than the rule for a bird to venture to the part of the tree where the sawfly is feeding, with the result that in general the larvae are not found, even though birds may be relatively abundant. If this explanation is correct, then we may expect that birds will be most effective in controlling insects that feed on parts of trees most accessible to them.

CONCLUSION

This study has shown that the effect of birds in environmental resistance is relatively slight so far as the larch sawfly is concerned because the sawfly larvae are found for the most part on the slender, flexible twigs far out at the end of the branches where the birds do not ordinarily go. Merely because they fail to destroy many sawfly larvae we are not justified in assuming that they would also have little effect upon other forms of insect life. In fact, it seems highly probable that birds might be extremely effective in reducing the number of insects under other circumstances, their effectiveness being directly proportional to the accessibility of their prey.

In addition to data concerned with the interrelation of birds and larch sawfly larvae, this study has brought out some interesting features of local bird distribution during the nesting season. During that period bird life was scattered more or less evenly over the area studied regardless of differences in forest type. The species varied from place to place, but the per acre concentration of the bird population appeared to be relatively uniform throughout the locality. It is probable that this degree of concentration will vary in different localities, depending on the amount of available food and cover. Perhaps four plus pairs per acre represents the degree of saturation possible in the locality studied. If this is true, then how can we bring about conditions that will make possible a higher degree of saturation with a resulting increase in the effectiveness of birds as a factor of environmental resistance?

Here we have opened up a wide field of profitable investigation for both the ornithologist and the forest entomologist, a field filled with possibilities both in the pure and applied phases. It would be difficult to find a more fascinating subject for investigation or a more profitable field of endeavor than this.

UNIVERSITY OF MICHIGAN

LIFE-HISTORIES OF MICHIGAN HALIPLIDAE (COLEOPTERA) *

JENNINGS R. HICKMAN

THE immature stages of the Haliplidae occurring in this country have received but little study. In fact, instars of only three species have been described. This work was done by Matheson (1912, pp. 178–191), and his observations on two haliplids were confirmed by Wilson (1923, pp. 271–275). This comprises the life-histories known for the different species of Haliplidae that are found in America. A general survey of the family was begun in the fall of 1924 and has been continued until the present time. Primarily, the Michigan haliplids, especially those occurring in the vicinity of Ann Arbor and the University of Michigan Biological Station at Douglas Lake, Michigan, have been studied. All the species known for Michigan have been reared by the author and the various stages examined in detail. On the following pages will be found descriptions of the different instars for *Peltodytes lengi* Rbts., *Peltodytes sexmaculatus* Rbts., *Peltodytes edentulus* Lec., *Haliplus immaculicollis* Harr., *Haliplus cribrarius* Lec. and *Haliplus triopsis* Say. Descriptions of the egg and first instar, however, are lacking for each of the last two species.

TECHNIQUE

The living stages were killed in boiling water and passed through the lower percentages of alcohol to 85 per cent. The material was prepared for study by first clearing it in hot 10 per cent caustic potash, washing it in water, and then transferring it to 85 per cent alcohol in Syracuse watch-glasses. In the drawings, general outlines and the locations of various structures were made with the aid of a camera lucida. The first and third larval instars were emphasized in the descriptions and only those structures of the second are mentioned that were different from the other two. Whenever possible, repetition was avoided. Permanent mounts were made of the dissected parts and deposited in the author's collection. A series of total alcoholic specimens were deposited in the Museum of the University of Michigan, the zoölogical collection of the Department of Zoölogy of the University of Michigan and the author's collections.

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* Contribution from the Zoölogical Laboratory and the Biological Station of the University of Michigan.

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PELTODYTES LENGI Roberts

EGG (Pl. XLVII, Figs. 1–4)

Size. — Length, 0.415–0.483 mm., average of 10 eggs 0.453 mm.; diameter, 0.231–0.289 mm., average of 10 eggs, 0.266 mm. Length increasing and diameter decreasing with development.

Shape. — Oval, with small, projecting plug (micropylar area) at anterior end. Chorion thin; superficially smooth, but under magnification faintly yet definitely reticulate; reticulation composed of polygonal units varying in shape and size; each reticulation unit in form of minute circular depression giving granular appearance to surface. Micropylar area circular; extending slightly beyond surface of chorion; composed of four to eight openings.

Color. — Yellowish-brown. Few days before hatching, six ocelli in one group, appearing on each side through the chorion as reddish-black spots.

LARVA

First Larval Instar (Pl. XLVII, Figs. 5–7)

Recently hatched larva. — Length of body, 0.65–0.80 mm., average of 10 specimens, 0.75 mm. Width of head, 0.38–0.48 mm., average of 10 specimens, 0.42 mm. Body broadest at head; thorax and abdomen tapering posteriorad. Body color milky-white; tips of mandibles yellowish-brown; ocelli dark brown. Appearance differing markedly from older larvae in much greater relative length of legs and dorsal projections. Principal internal structures evident through translucent integument.

Five-day larva.—Size rapidly increasing to second moult. Body length including caudal projections, 1.68–2.31 mm., average of 10 specimens, 2.11 mm.; width of head, 0.42–0.502 mm., average of 10 specimens, 0.46 mm. Length of terminal segment, 0.168–0.21 mm., average of 10 specimens, 0.186 mm. Length of caudal projections, 0.504–0.756 mm., average of 10 specimens, 0.672 mm. Body broadest at head; thorax and abdomen tapering slightly posteriorad. Body surface, exclusive of projections and setae, very smooth.

Head capsule. — Epicranial suture very indistinct; junction of arms at posterior border of head; stem very short. Setae moderately long, situated on each side as follows: two on epistomal margin, outer one longest; one near median line in region of frons; three above antenna; two adjacent to arm of epicranial suture; one above and one posterior to ocular stalk; five on ocellar protuberance; one ventrad to antenna; two on region of submentum.

Ocelli. — Six globular ocelli in circle on strong lateral protuberance; color dark brown. Size and shape not uniform.

Antenna (Pl. XLVII, Fig. 5). — Three-segmented; first segment about as wide as long; second more than three times as long as first, widest at middle; third about as long as second, but about half as wide. Second with very short appendage on inner, distal margin. Two setae on distal end of third segment, one about as long as third segment and one very short.

Mandible (Pl. XLVII, Fig. 6). — About as wide as long; strong apical tooth-like structure larger on left than right; two setae on external margin.

Maxilla. — Twice as long as wide; with three setae, two-segmented palpus, second the longer; group of setae on cephalomedian margin.

Labium. — Rounded on free margin; two-segmented palpus; no setae.

Prothorax. — Longest of body segments; smooth; weakly chitinized. Four two-segmented projections, two lateral and two dorsal; very long and slender; length more than twice the width of body; first segment shorter; covered with granular projections; second segment smooth. Lateral projections with one long seta distal from first segment, and one spine near base. Eight strong setae dorso-cephalad; four setae further posteriorad.

Meso- and metathorax. — Projections and appearance same as in prothorax. Two setae between lateral and dorsal projections on each side, inner one longer; one seta at base of each dorsal projection.

Abdomen. — Nine-segmented; dorsal aspect of first eight segments similar except in decrease in width caudad; smooth; weakly chitinized. Each segment with four long two-segmented projections, similar to those on thorax with exception that first segment of lateral projections lacks long terminal seta. Two small setae on each side between lateral and dorsal projections; one at base of each dorsal projection. Ninth segment terminating in two long cercus-like projections; each caudal projection with four lateral and one terminal setae; equal in length to last three abdominal segments.

Ventral aspect of segments. — Thoracic segments without setae except four on cephalic margin of prothorax. First eight segments of abdomen with four setae on ventral aspect of each and two on each side in region of pleurum. Ninth segment with prominent rounded protuberance with anal opening near median line.

Legs. — First thoracic leg very short; half as long as third; fitted for grasping; consisting of coxa, trochanter, femur, tibia, tarsus and claw. Number and arrangement of setae similar to those found in third instar. Second and third thoracic legs similar except third slightly longer. Number and arrangement of setae similar to those in third instar.

Spiracles. — Absent. Tracheae extending into the long dorsal and lateral projections.

Second Larval Instar (Pl. XLVIII, Fig. 8)

Body length, including caudal projections, 2.8–4.2 mm., average of 10 specimens, 3. 36 mm. Width of head, 0.56–0.58 mm., average of 10 specimens, 0.57 mm. Length of terminal segment, 0.21–0.34 mm., average of 10 specimens, 0.29 mm. Length of caudal projections, 1.05–1.5 mm., average of 10 specimens, 1.26 mm. Larva more closely resembling third larval instar. Body very smooth except for projections and setae.

Antenna. — Three-segmented, but third segment composed of two terminal, parallel, diminutive, subequal projections.

Mandibles. — External margin with three setae.

Dorsal aspect of prothorax. — Four long projections, of nine segments each, over 2 mm. long. First segment of each projection with two prominent spines. Six prominent dorsal setae near cephalic margin.

Dorsal aspect of meso- and metathorax. — Similar to prothorax except cephalic setae lacking and only one spine on first segment of projection. (The length of this spine proves to be a useful character in separating species. In this species the length of this spine is equal to the thickness of projection which bears it. Its length is 0.021 mm.)

Abdomen. — Nine segments. Dorsal aspect of first six segments with four long projections similar to those of thorax. Number of segments in projections 8–10. Dorsal aspect of seventh and eighth segments each with two long dorsal projections and two short, lateral, stub-like projections. Ninth segment with two long projections directed posteriorad; projection composed of six segments, each with one seta on latero-distal margin; one seta on distal end of terminal segment. First segments of caudal projection with seven scattered setae. Ventral aspect of thoracic segment with seta-bearing projection near base of coxa of each pair of legs (not shown in Fig. 8). First eight segments of abdomen with six ventral setae, median two the largest; also five setae on each side of lateral aspect, in two groups of two (anterior) and three (posterior). No spiracles; trachea extending into long dorsal and lateral projections to tip.

Third Larval Instar (Pl. XLIX, Fig. 9; Pl. L, Figs. 10–17, 19)

Body length including caudal projections, 9.1–11.3 mm., average of 10 specimens, 10.5 mm. Width of head, 0.71–0.75 mm., average of 10 specimens, 0.73 mm. Length of terminal segment, 0.38–0.42 mm., average of 10 specimens, 0.40 mm. Length of caudal projections, 4.83–5.1 mm., average of 10 specimens, 4.96 mm. Color of body light yellow. Head light brown. Tips of mandibles dark brown. Ocelli blackish.

Head capsule (Pl. L, Fig. 10). — Trapezoidal; prognathous; slightly flattened above; more globular below. Arms of epicranial suture convergent behind; suture very short. Capsule interspersed with short setae inserted upon small protuberances.

Ocelli (Pl. L, Fig. 11). — Six, arranged in circle upon prominent lateral protuberance.

Antenna (Pl. L, Fig. 12). — Laterad; cephalad to ocelli; on protuberance; four segments; filamentous; light amber in color. Scape slightly wider than long; with few sense pits on distal margin. Pedicel one fourth longer than scape, but little narrower. Two-segmented flagellum about one and one-half times as long as scape and pedicel combined; first segment about three times as long as second; bobbin-shaped; greatest diameter proximal; small sense pore on disto-lateral margin; second segment composed of two diminutive, parallel, terminal, subequal parts; inner part shorter, conical; outer part rectangular, bearing seta at apex; seta slightly longer than segment.

Mandibles (Pl. L, Fig. 13). — Asymmetrical; fairly prominent with rather sharp beak-like tip; three fourths as wide as long; outer margin convex with six rather large setae, proximal one shortest; two sense pores on dorso-lateral aspect. Tooth-like projection on each inner margin. Orifice of suction canal irregular; on ventral side of beak. Condyle small; triangular; short; no neck. Left mandible slightly larger than right; left beak distinctly larger than right.

Maxilla (Pl. L, Fig. 14). — Cardo rectangular with one seta on cephalo-lateral margin. Stipes about as long as wide with five setae in two transverse rows; palpus two-segmented; second segment about as long as first; first with two setae and ring of sense pores on distal margin; distal margin of stipes with pointed projection covered with fine setae; two knife-like projections on cephalo-mesal margin.

Labium (Pl. L, Fig. 15). — Short; rectangular; with two setae on mentum area; palpus two-segmented; first segment very short with one seta; second segment blunt.

Prothorax. — Longest segment; great number of short setigerous tubercles on cephalic region; bearing six long segmented projections on dorsal aspect, two lateral, two dorsal and two dorso-lateral. Lateral and dorsal projections with about fourteen segments. Two prominent and several smaller spines on first segment of lateral and dorsal projections. First three segments of lateral and dorsal projections with whorl of tiny angular processes around distal margin; remaining segments smooth. Dorso-lateral projections with about twelve segments.

Dorsal aspect of meso- and metathorax. — Mesothorax and metathorax similar; each with four long projections of 16–18 segments, first segment with two prominent spines. (These spines prove to be useful characters in separating species. In this species the length of the spine is equal to the thickness of projection which bears it. Length, 0.042 mm.) First three segments of projections have whorl of tiny angular processes on distal margin. One seta between dorsal and lateral projection.

Dorsal aspect of first seven abdominal segments. — With four long 16–18 segmented projections. Projections similar to those of thorax except one seta on first segment of lateral projection. Eighth abdominal segment with two long dorsal projections and two lateral stub-like processes. Ninth abdominal segment subcylindrical terminating in two cylindrical, divergent, about 8–12 segmented projections, about as long as whole abdomen. (The number of segments in the terminal projections varies widely even in the pair of the same individual.) Basal segment of terminal projection long, with many setigerous tubercles largely on proximal half; each succeeding segment except terminal one with one seta, usually laterad; segments gradually tapering to thread-like terminations.

Ventral aspect of prothorax. — Without setae. Mesothorax and metathorax with two setigerous tubercles on median line.

Ventral aspect of abdomen. — With 8–10 setigerous tubercles on each segment, arranged in transverse rows; also several small setae scattered irregularly.

Lateral aspect of each abdominal segment. — With three prominent setae. Spiracles present; one pair on mesothorax and one pair on each of first seven abdominal segments.

First pair of thoracic legs (Pl. L, Figs. 16–17). — Rather short; prehensile; composed of coxa, trochanter, femur, tibia, tarsus and claw. Coxa longest, tapering distad; distal margin incurved on dorsal side to allow bending back of trochanter; about as long as wide; several prominent setae on distal and proximal margins. Trochanter not quite as long as coxa, but twice as long as wide; convex on ventral side, concave on dorsal side; transverse row of sense pores mesad; one seta on dorsal face, five on ventral face, distal one longest. Femur one and one-half times as long as trochanter and about half as wide as long; four setae on dorsal face; several others scattered on both sides. Tibia slightly shorter than femur; ventro-distal margin expanding into thumb-like process; distal surface of latter serrated; one seta on each side at base of process, one on ventral aspect near apex, and one strong seta on apex; serrations or processes large at base and becoming smaller distad. Tarsus about two thirds as long as tibia and two thirds as wide; few setae on distal margin, and one group on disto-ventral aspect. Claw as long as tarsus; rather sharp, with setigerous tubercle on ventral face; one seta just proximad of tubercle.

Second and third thoracic legs. — Similar; about twice as long as first; proportions of segments to each other about same as for first; distribution of setae similar to that of first legs; tibiae without distal process. Adapted for walking.

PUPA (Pl. L, Figs. 22–23)

Typical exarate pupa. Total length, 3.45–3.60 mm., average of 5 specimens, 3.57 mm.· Width including wings, 2.05–2.12 mm., average of 5 specimens, 2.1 mm. Length of pronotum, 0.72–0.82 mm.. average of 5 specimens, 0.8 mm. Width of pronotum, 1.21–

1.28 mm., average of 5 specimens, 1.26 mm. Shape, oval, distinctly enlarged at mid-section. Body color, light cream. Eyes, reddish-black. Setae of different lengths, mostly inserted upon short tubercles. Ocelli, six; arranged in two compact rows just within lateral margin of compound eyes. Head with one short seta slightly above each antenna and two on vertex. Antennae diagonally across eyes. Pronotum longest; with ten long setae and two short ones, arranged as follows: six long ones on cephalic margin and four long ones on caudal margin; two short ones on caudal margin. Mesonotum and metanotum with four short setae each. Abdomen with nine segments; transverse section decreasing rapidly caudad. First six segments each with two long setae and four short ones. Seventh segment with four short setae; eighth with six, and ninth with twelve. First and second legs folded upon themselves at femuro-tibial joint; one seta at this joint. Third legs straight, projecting slightly beyond abdomen. Tube-like spiracles on second, third and fourth segments.

PELTODYTES SEXMACULATUS Roberts

EGG

The eggs of *P. sexmaculatus* Rbts., *P. lengi* Rbts. and *P. edentulus* Lec. are so nearly identical in appearance that the author was unable to detect any structural features by means of which these three could be separated, in spite of the fact that all structural features were critically studied. Therefore, the description given for the egg of *P. lengi* Rbts. will serve for that of *P. sexmaculatus* Rbts.

LARVA

First Larval Instar

Here again the first larval instars of *P. sexmaculatus* Rbts., *P. lengi* Rbts. and *P. edentulus* Lec. are so nearly identical in appearance that the author was unable to find differences in structures by which these three could be separated. The description given for the first larval instar of *P. lengi* Rbts. will serve for that of *P. sexmaculatus* Rbts.

Second Larval Instar

The only observed difference in the larval structures of this instar from those of *Peltodytes lengi* Rbts. and *P. edentulus* Lec. is in the length of the spine on the dorsal projections. It is much longer and more pointed than in the other two, the length being about one and one-third times the diameter of the projection.

Third Larval Instar

The only observed difference in the larval structures of this instar when compared with that of *Peltodytes lengi* Rbts. and *P. edentulus* Lec. is the same feature already described above under the heading "Second larval instar."

PUPA

Structural features of the pupae of *P. sexmaculatus* Rbts., *P. lengi* Rbts. and *P. edentulus* Lec. were identical, as far as the author was able to determine. Therefore, the description given for *P. lengi* Rbts. will serve for that of *P. sexmaculatus* Rbts.

PELTODYTES EDENTULUS Leconte

EGG

The description given for the egg of *P. lengi* Rbts. will serve for that of *P. edentulus* Lec., since no differences could be observed between eggs of these two species.

LARVA

First Larval Instar

Since the first larval instars of *P. sexmaculatus* Rbts. are so nearly identical to those of *P. lengi* Rbts., it is not necessary to give a description of this instar.

Second Larval Instar

The only structure observed to be different in this instar from those of *Peltodytes lengi* Rbts. and *P. sexmaculatus* Rbts. is in the length of spine on the dorsal projections. It is much shorter than in the other two, the length being about two thirds the thickness of the projection.

Third Larval Instar

This instar was found to differ from *Peltodytes lengi* Rbts. and *P. sexmaculatus* Rbts. only in the same feature already described above under the heading "Second larval instar."

PUPA

Structural features of the pupae of *Peltodytes edentulus* Lec., *P. lengi* Rbts. and *P. sexmaculatus* Rbts. were identical as far as the author was able to determine. Therefore the description given for *P. lengi* Rbts. will serve for that of *P. edentulus* Rbts.

HALIPLUS IMMACULICOLLIS Harris

EGG (Pl. LI, Fig. 24)

Size. — Length, 0.338–0.386 mm., average of 10 eggs, 0.368 mm.; diameter, 0.212–0.231 mm.; average of 10 eggs, 0.224 mm.

Shape. — Similar to the eggs of the described species of the genus *Peltodytes.*

Color. — Whitish. Six ocelli in one group; appearing on each side through chorion as reddish-black spots.

LARVA

First Larval Instar (Pl. LI, Figs. 25–27)

Recently hatched larva. — Length of body, 1.4–1.8 mm., average of 5 specimens, 1.6 mm. Width of head, 0.164–0.172 mm., average of 5 specimens, 0.168 mm. Head slightly narrower than thorax. Body segments, 13, tapering gradually posteriorad. Color milky-white with exception of yellowish-brown mandible tips and dark brown ocelli. Body very compact and resembling first larval instar of *Peltodytes lengi* Rbts., *P. sexmaculatus* Rbts. and *P. edentulus* Lec. Integument translucent, principal internal structures showing through.

Older larva. — Body length including caudal projections, 2.3–3.12 mm., average of 5 specimens 2.86 mm.; width of head, 0.19–0.23 mm., average of 5 specimens, 0.21 mm. Length of terminal segment, 0.35–0.45 mm., average of 5 specimens, 0.42 mm. Length of caudal projections, 0.25–0.32 mm., average of 5 specimens, 0.29

mm. Body much longer and resembling later instars of same species.

Head capsule. — With very indistinct epicranial suture; arms of suture uniting at caudal edge of head; stem of suture very short. Both dorsal and ventral aspects of surface with small round tubercles. Setae usually on rather prominent projections arranged on each side as follows: two behind ocellar area and two laterad to epicranial suture; two small ones near median line in region of frons; several small setae on cephalic margin of head; one below antenna and two on region of submentum.

Ocelli. — Six; globular; one slightly cephalo-ventrad to antenna; remaining five in two vertical rows, cephalic row with two and caudal with three.

Antenna (Pl. LI, Fig. 26). — With four segments; similar to that of mature larva except outer part of fourth segment and terminal seta are longer proportionately.

Mandible. — Slightly longer than wide with one seta on external margin; apical tooth strong.

Maxilla. — Twice as long as wide. Palpus, three-segmented; third segment longest. One group of setae on anterior margin.

Labium. — Rounded on free margins; palpus, two-segmented; no setae.

Prothorax. — Longest segment. Dorsal aspect with twenty setigerous tubercles, arranged in six rows, two dorsal rows of three each, two lateral rows of five each, and two dorso-lateral rows of two each.

Meso- and metathorax. — Similar, with ten setigerous tubercles situated as follows: two dorsal rows of two each, caudal one longest; lateral row of two each, caudal one with the very long seta and dorso-lateral one very short.

Abdomen. — Ten segments. Dorsal aspect of first seven segments similar; each with eight setigerous tubercles; two dorsal rows with two each, caudal one longest; one laterad, and one dorso-laterad; setae on lateral ones longer than others. Eighth and ninth segments with six setigerous tubercles; two dorsal rows with two each, one seta laterad. Setigerous tubercles of each body segment on plate more heavily chitinized than rest of body wall; plate also granulose. Tenth segment (Pl. LI, Fig. 27) slightly longer than others, terminating in two projections, each with one lateral and one terminal seta; surface also granulose.

Ventral aspect of each thoracic segment. — With one setigerous tubercle laterad to coxa. Ventral aspect of first nine abdominal segments with four rather prominent setae in transverse row; one group of setae on each side. Anal protuberances not very prominent; consisting of one and two lateral lobes.

Legs. — Similar in shape and arrangement of setae to those of mature larva. Spiracles absent.

Second Larval Instar (Pl. LI, Figs. 28–29)

Larva very similar to third instar and quite different from first. Body length including caudal projections, 3.36–4.41 mm., average of 5 specimens, 4.25 mm. Width of head, 0.294–0.336 mm., average of 5 specimens, 0.315 mm. Length of terminal segments, 0.84–0.105 mm., average of 5 specimens, 0.92 mm. Length of caudal projections, 0.25–0.336 mm., average of 5 specimens, 0.28 mm. Conspicuous change in number, form and arrangement of setigerous tubercles on dorsal and ventral aspect of body segments. Dorsal aspect of prothorax with six longitudinal rows of tubercles; also several on cephalic margin; tubercles of lateral rows numerous, those of dorso-lateral rows fewer; two long setae on caudal margin and three on cephalic margin. Mesothorax and metathorax with same number of rows, but with fewer tubercles; 6–8 tubercles in lateral row, 3–4 in dorsal, and 2–3 in dorso-lateral rows; one long seta in lateral row. Nine abdominal segments like mesothorax and metathorax; number of tubercles variable, but always more on lateral row; tenth segment greatly elongated, with numerous setigerous tubercles. Each caudal projection with seven lateral setae and one terminal seta. Ventral aspect of abdominal segments with five setigerous tubercles arranged in inverted V-shaped figure; also four others with shorter tubercles and longer setae. Lateral aspects with four setae on each side, two closely grouped together.

Third Larval Instar (Pl. LII, Figs. 30–39)

Body length including caudal projections, 7.42–7.85 mm., average of 5 specimens, 7.62 mm. Width of head, 0.30–0.42 mm., average of 5 specimens, 0.35 mm. Length of terminal segment, 1.72–1.85 mm., average of 5 specimens, 1.8 mm. Length of caudal projections, 0.38–0.42 mm., average of 5 specimens, 0.40 mm. Body with bluish-black, mid-dorsal stripe; head light brown; tips of mandibles dark brown; ocelli blackish.

Head capsule. — With indistinct epicranial suture; arms of suture convergent near caudal margin of capsule; stem very short. Four prominent setigerous tubercles on capsule; two posteriorad to ocellar area; two laterad to epicranial suture. Several setae scattered over capsule.

Ocelli. — Six; five grouped together in imperfect semicircle posteriorad to antenna. Sixth, ventro-cephalad to antenna.

Antenna (Pl. LII, Fig. 32). — Dorso-cephalad to ocellar area; four segments, filiform. Scape slightly wider than long; few sense pores on distal margin. Pedicel one fourth longer than scape, but a little narrower. Flagellum two-segmented; one and one-half times longer than scape and pedicel combined; first segment longest, more than four times the second, bobbin-shaped, greatest diameter slightly distad of middle; one long seta on latero-distal margin. Terminal segment composed of two diminutive, parallel, subequal parts; inner part shorter, conical; outer part rectangular, bearing seta at apex; seta about twice as long as segment.

Mandible (Pl. LII, Fig. 33). — About as long as wide; strongly elliptical in cross-section; outer face convex with four rather stout setae; proximal one shortest; strong apical tooth. Orifice of suction canal on ventral side of tooth. Inner face with sharply pointed projection; condyle round, with short neck. Tooth of left mandible slightly longer than right.

Maxilla (Pl. LII, Fig. 34). — With simple cardo; triangular; one seta on lateral aspect. Stipes twice as long as wide; rectangular. Palpus three-segmented; third segment as long as first two; second with three setae. Distal margin with many setae. Disto-mesal margin with notch and two stout setae.

Labium (Pl. LII, Fig. 35). — Rounded; two setae on ventral aspect. Palpus two-segmented, second slightly longer than first. Distal margin with four setae.

Dorsal aspect of prothorax. — Unlike other segments. Prothorax longest; with many more setigerous tubercles; cephalic area thickly covered. Shallow depressions on each side of meson. Setigerous tubercles in six rows, becoming more distinct on caudal region. Terminal tubercles branched.

Dorsal aspect of meso- and metathorax. — Very similar in appearance. Setigerous tubercles in six rows. One elongate seta in each of four median rows. Lateral margin rounded.

Dorsal aspect of first seven abdominal segments. —Similar. Setigerous tubercles in six rows; arrangement and number variable; rows tending to coalesce cephalad. Eighth segment with only four rows and ninth with but two. Tenth segment (Pl. LII, Fig. 36) greatly prolonged; caudal projections with six lateral setae and one terminal; whole segment, except projections, covered with small setigerous tubercles.

Ventral aspect of thorax. —With two setigerous tubercles laterad to each coxa. Coxa bounded cephalad with serrated chitinized plate.

Ventral aspect of abdomen. — With chitinized plate covered with setigerous tubercles.

Lateral aspect of each abdominal segment. —With one seta. Eight pairs of spiracles; one pair on mesothorax and seven pairs on the first seven abdominal segments.

First pair of thoracic legs (Pl. LII, Fig. 37–38). —Fitted for grasping, consisting of coxa, trochanter, femur, tibia, tarsus and claw. Coxa broadly inserted; decreased in size distad; thickest segment of leg; about twice as long as wide; few angular short spines on ventral face; several scattered smaller setae; one larger seta on disto-cephalic face. Trochanter, convexo-concave; about two thirds as long as coxa; with ring of sense pores near middle; one seta on dorsal face and several on ventral face, very long one near distal margin. Femur short, slightly longer than trochanter, but wider; several angular spines on ventral side; three setae on dorsal margin; two stout setae on ventro-cephalic face; few scattered setae on lateral areas. Tibia about three fourths as long as femur, with prolongation on disto-ventral face terminating in two stout tooth-like setae and few angular spines; two setae on disto-cephalic and caudal aspect, one on proximo-dorsal face and several angular spines near middle of dorsal face. Tarsus about one half as long as tibia, with small spines on disto-ventral aspect; several setae on distal margin and two on dorsal margin. Claw, one and one-half times as long as tarsus; tooth-like projection on ventral face.

Second and third pair of thoracic legs. — Similar to first except about twice as long and prolongation absent on tibia. Adapted for walking.

PUPA (Pl. LII, Fig. 39)

Total length, 2.07–2.12 mm., average of 5 specimens, 2.1 mm. Width including wings, 1.24–1.28 mm., average of 5 specimens, 1.26 mm. Length of pronotum, 0.41–0.44 mm., average of 5 specimens, 0.42 mm. Width of pronotum, 0.61–0.65 mm., average of 5 specimens, 0.63 mm. Shape oval; distinctly enlarged at midsection. Color, light cream, except reddish-black eyes. All setae of practically same length; inserted upon low tubercles. Ocelli six; grouped in straight line; laterad to compound eyes. Head with two rather short setae slightly above antenna and two on vertex. Antennae diagonally across eyes. Pronotum longest; with twelve setae, six on cephalic margin and six on caudal margin. Mesonotum and metanotum each with six setae. Abdomen with nine segments; tapering rapidly posteriorad. Each of first seven segments with eight setae all about same length and arranged in transverse row. Eighth segment with six setae and ninth with none. First and second legs folded at femuro-tibial joint; short seta on this joint. Third legs straight and extend slightly beyond abdomen. Tube-like spiracles on second, third and fourth segments.

HALIPLUS CRIBRARIUS Le Conte

Descriptions of the egg and first larval instar are lacking for this species, since the author was unable to secure them. The other stages, however, were obtained by collecting larvae of second instar and rearing them to the adult stage. The exuviae were saved and compared with the preserved material.

LARVA

Second Larval Instar (Pl. LIII, Fig. 40)

Body length including caudal projections, 4.3–5.6 mm.; average of 5 specimens, 4.8 mm. Width of head, 0.48–0.54 mm.; average of 5 specimens, 0.52 mm. Length of terminal segment, 0.91–1.05 mm.; average of 5 specimens, 0.95 mm. Length of caudal projections, 0.054–0.126 mm.; average of 5 specimens, 0.082 mm. Larva differing from third larval instar in number, form, and arrangement of setigerous tubercles on dorsal and ventral aspect of body segments. Dorsal aspect of prothorax with four, many-branched projections posteriorad, two lateral and two dorsal ones. Each branch terminating with one seta. One very long seta inserted on low tubercles on each lateral projection, one between lateral and dorsal projections, and one cephalad to each lateral projection. About thirty setigerous tubercles on cephalic region. Mesothorax and metathorax similar to prothorax except lacking cephalic setigerous tubercles. About fifteen setigerous tubercles on each lateral projection and about ten on each dorsal projection. First nine abdominal segments similar to mesothorax and metathorax. Tenth abdominal segment greatly elongated, with numerous setigerous tubercles. Each caudal projection with four setigerous tubercles, and one terminal seta. Ventral aspect of abdominal segments with six setigerous tubercles in posterior transverse line. Lateral aspect of first eight abdominal segments with two closely grouped together setae on each side.

Third Larval Instar (Pl. LIV, Figs. 42–50)

Body length including caudal projections, 11.3–12.5 mm.; average of 10 specimens, 12 mm. Width of head, 0.63–0.67 mm.; average of 10 specimens, 0.65 mm. Length of terminal segment, 3.36–3.62 mm.; average of 10 specimens, 3.48 mm. Length of caudal projections, 0.16–0.18 mm.; average of 10 specimens, 0.17 mm. Body subcylindrical; tapering posteriorad from thorax to tip of prolonged caudal segment. Body amber color; head slightly darker; tips of mandibles dark brown; ocelli blackish.

Head capsule (Pl. LIV, Fig. 43). — Rectangular in dorsal outline; slightly wider than long. Prognathous. Epicranial suture very indistinct. Granular elevations covering entire capsule. Few scattered setae; one prominent, hook-shaped setigerous tubercle posteriorad to each ocellar area.

Ocelli (Pl. LIV, Fig. 44). — Six; grouped together in two vertical rows; unequal; slightly projecting.

Antenna (Pl. LIV, Fig. 45). — Dorso-cephalad to ocellar area; four-segmented; filiform. Scape slightly wider than long, few sense pores on distal margin. Pedicel one third longer than scape, but a little narrower. Flagellum, two-segmented; about twice as long as scape and pedicel combined; first segment more than four times longer than second, bobbin-shaped; one seta on latero-distal margin. Terminal segment composed of two, diminutive, parallel, subequal parts; inner part slightly longer, conical; outer part rectangular, bearing seta at apex; seta about as long as segment.

Mandibles. — Hook-shaped; about one fifth longer than wide; lateral margin convex. Two setae on lateral margin, proximal one shorter than distal one. Strong apical tooth. Orifice of suction canal on ventral side of tooth. Inner face with sharply pointed projection. Condyle round, with short neck. Tooth of left mandible slightly longer than right.

Maxilla (Pl. LIV, Fig. 46). — With cardo simple; free; subtriangular; one seta on ventro-lateral aspect. Stipes subtrapezoidal; large; about as long as wide; two parallel rows of setae on lateral margin; three in each row; group of both stout and fine setae on meso-distal margin, stout ones mesad to group. Maxillary palpus three-segmented; basal segment slightly wider than long, one seta on lateral margin; second segment about as long as basal, not quite so wide; with two setae; apical segment conical, one third longer than second, twice as long as wide, sensory organs on apex.

Labium (Pl. LIV, Fig. 47). — Rectangular, about two times wider than long; two setae on mentum area. Labial palpus of two segments, proximal segment as long as wide; distal segment conical, slightly longer than proximal segment, but narrower; four setae on distal margin of labium.

Prothorax. — About twice as wide as head, and twice as long; bears four long, stout, blunt pointed, horn-like processes. Dorsal and lateral surface of processes densely covered with setigerous tubercles. Processes terminate with heavily chitinized point. Cephalic region of prothorax bearing numerous setigerous tubercles. Ten long, scattered setae on segment.

Dorsal aspect of meso- and metathorax.—Similar. Each segment with four horn-like processes, similar to those of prothorax. Three half-round protuberances on cephalic area, with fine angular spines. Each segment with six long setae.

Dorsal aspect of first nine abdominal segments. — Similar, except tapering posteriorad; number and arrangement of horn-like processes and long setae similar to mesothorax and metathorax. Tenth abdominal segment very long and tapering, covered with setigerous tubercles; end of segment bifid very short distance (one twentieth of total length); terminating with long, stout setae. One setigerous tubercle on each branch.

Ventral aspect of thorax. — With several setigerous tubercles; each coxa bounded cephalad with serrated chitinized plate.

Ventral aspect of first nine abdominal segments. — With chitinized plate covering about one half of surface of each segment. Each plate covered rather sparsely with setigerous tubercles. Similar to dorsal ones, but shorter. Eight pairs of spiracles, one pair on mesothorax, and rest on first seven abdominal segments on lateral aspect. One group of two setae on lateral aspect of first nine abdominal segments.

First pair of thoracic legs. — Coxa, one and one-half times longer than wide. Group of triangular granular elevations on proximo-ventral aspect. Several strong, scattered setae on all faces. Trochanter twice as long as wide; convexo-concave; ventral aspect with five long setae, and numerous short spines; median row of sensory pits. Femur more than twice as long as wide, club-shaped, with large end distal, covered with numerous short spines on ventral aspect. Several scattered setae on dorsal aspect. Tibia a little more than twice as long as wide, two thirds as long as femur; almost completely covered with rather regularly placed short spines; several long setae on distal margin. Tarsus three fourths as long as tibia; several short, subrectangular elevations on dorsal and ventral aspects; rather long and stout setae distad. Claw one and one-fourth times as long as tarsus, tapering to rather sharp point; group of four spines on ventral margin.

Second and third pairs of thoracic legs. — Similar to first, except longer; adapted for walking.

PUPA

Total length, 3.72–3.81 mm.; average of 3 specimens, 3.78 mm. Width including wings, 1.64–1.69 mm.; average of 3 specimens, 1.68 mm. Length of pronotum, 1.04–1.06 mm.; average of 3 specimens, 1.05 mm. Width of pronotum, 0.83–0.85 mm.; average of 3 specimens, 0.84 mm. Size was the only observed difference between this species and *H. triopsis.* This species was somewhat larger. There are only six setae on the dorsal aspect of the first seven abdominal segments, as was true of *H. triopsis.*

HALIPLUS TRIOPSIS Say

Since the author was unable to obtain eggs of this species, the descriptions of the different stages that are given are based on a comparison of the exuviae of reared specimens and the preserved material that had been collected. No larvae of the first instar were taken in the field.

LARVA

Second Larval Instar (Pl. LIII, Fig. 41)

Body length including caudal projections, 5.46–5.88 mm.; average of 5 specimens, 5.67 mm. Width of head, 0.42–0.504 mm.; average of 5 specimens, 0.462 mm. Length of terminal segment, 1.47–1.76 mm.; average of 5 specimens, 1.67 mm. Length of caudal projections, 0.294–0.378 mm.; average of 5 specimens, 0.336 mm. Larva differing from third instar in number, form and arrangement of setigerous tubercles on dorsal and ventral aspect of body segments. Dorsal aspect of prothorax with four strong, many-branched setigerous tubercles posteriorad, two lateral and two dorsal ones; one long setigerous tubercle dorso-latero-posteriorad; several setigerous tubercles on cephalic region; twelve scattered long setae inserted on low tubercles. Mesothorax and metathorax similar to prothorax except lacking cephalic setigerous tubercles; number of setigerous tubercles about thirty on each segment; four long setae inserted on low tubercles. First nine abdominal segments similar to mesothorax and metathorax. Tenth abdominal segment greatly elongated, with numerous setigerous tubercles. Each of caudal projections with four setigerous tubercles and one terminal seta. Ventral aspect of abdominal segments with six setigerous tubercles in posterior transverse line. Lateral aspects of first eight abdominal segments with two setae closely grouped on each side.

Third Larval Instar (Pl. LV, Figs. 51–59)

Body length including caudal projections, 5.88–13.44 mm.; average for 10 specimens, 12.6 mm. Width of head, 0.546–0.63 mm.; average for 10 specimens, 0.588 mm. Length of terminal segment, 3.57–3.99 mm.; average of 10 specimens, 3.78 mm. Length of caudal projections, 0.16–0.21 mm.; average of 10 specimens, 0.18 mm. Body subcylindrical, tapering caudad from thorax to tip of prolonged caudal segment. Setigerous tubercles on body; amber brown; rest of body cream yellow; head amber brown; tips of mandibles dark brown; ocelli blackish.

Head capsule (Pl. LV, Fig. 52). — Subrectangular in dorsal outline; slightly wider than long; prognathous. Epicranial suture very indistinct. Several scattered patches of granular elevations. Few dispersed setae, both long and short; one prominent, hook-shaped, setigerous tubercle on each side just caudad to ocellar area.

Ocelli (Pl. LV, Fig. 53). — Six; grouped together in two imperfect vertical rows posteriorad to antenna; unequal; each slightly protruding.

Antenna (Pl. LV, Fig. 54). — Cephalad to ocellar area; four segments; filiform; incurved. Scape slightly wider than long; few sense pores on distal margin. Pedicel one third longer than scape, but a little narrower. Flagellum two-segmented; more than twice as long as scape and pedicel combined; first segment longest, more than four times the second; bobbin-shaped; one seta on latero-distal margin. Terminal segment composed of two diminutive, parallel, subequal parts; inner part slightly longer, conical;

outer part rectangular, bearing seta at apex; seta slightly longer than segment.

Mandibles (Pl. LV, Fig. 55). — Hook-shaped; about one fourth longer than wide; lateral margin convex, with two setae. Strong apical tooth. Orifice of suction canal on ventral side of tooth elliptical. Inner face with three sharply pointed projections. Condyle round, with short neck. Tooth of left mandible slightly longer than right.

Maxilla (Pl. LV, Fig. 56). — With simple cardo; free; triangular; one seta on lateral aspect. Stipes subtrapezoidal; slightly longer than wide; seven unequal setae on latero-ventral aspect. Palpus three-segmented; second and third segments about equal; second with two setae; third with sensory pits on apex. Distal margin with many fine setae. Disto-mesal margin with two stout setae.

Labium (Pl. LV, Fig. 57). — Rounded; submentum area with two groups of six setae in each. Mentum with two setae. Palpus two-segmented, second slightly longer than first. Group of three setae at base of each palpus. Two groups of three each on distal margin.

Prothorax. — Unlike other segments; longest; almost entire surface covered with setigerous tubercles with six branched setigerous tubercles posteriorad. Shallow depression free from tubercles on each side of meson.

Dorsal aspect of meso- and metathorax. — Very similar in appearance. Setigerous tubercles covering entire surface, with six branched tubercles posteriorad.

Dorsal aspect of first seven abdominal segments. — Similar to mesothorax and metathorax. Eighth and ninth segments with only four branched setigerous tubercles. Tenth segment (Pl. LV, Fig. 58) greatly prolonged; covered with setigerous tubercles; bifid at terminal end. Each branch very short, about one nineteenth of total length; each with two setigerous tubercles, one seta on side and one terminal seta.

Ventral aspect of thorax. — With two setigerous tubercles laterad to each coxa. Coxa bounded cephalad with serrated chitinized plate.

Ventral aspect of abdomen. — With chitinized plate covered with setigerous tubercles.

Lateral aspect of each abdominal segment. — With two setae, grouped together on each side of first nine segments. Eight pairs of spiracles; one pair on mesothorax and seven pairs on the first seven abdominal segments.

First pair of thoracic legs (Pl. LV, Fig. 59). — Not fitted for grasping; consisting of coxa, trochanter, femur, tibia, tarsus and claw. Coxa largest segment; broadly inserted; decreased in size distad; more than twice as long as wide; few scattered setae. Trochanter convexo-concave; about half as long as coxa; with ring of sense pores near middle; one seta on dorsal face, and several on ventral and lateral faces. Femur stout, about as long as coxa; row of several setae on dorsal face, and many scattered setae and angular projections on ventral face. Tibia about two thirds as long as femur; convex dorsal and ventral margins; several stout setae on distal margin; group of short, angular projections on disto-ventral aspect. Tarsus slightly shorter than tibia; several setae on distal margin, and short angular projections on ventral and dorsal aspect. Claw slightly longer than tarsus; two long, and two short tooth-like projections on ventral margin.

Second and third pairs of thoracic legs. — Similar to first, except a little longer. Adapted for walking.

PUPA

Total length, 3.27–3.40 mm.; average of 3 specimens, 3.36 mm. Width including wings, 1.81–1.88 mm.; average of 3 specimens, 1.86 mm. Length of pronotum, 0.41–0.43 mm.; average of 3 specimens, 0.42 mm. Width of pronotum, 0.59–0.67 mm.; average of 3 specimens, 0.63 mm. Structural features of this species are the same as those of *H. immaculicollis* Harr., except for the number of setae on abdomen. In *H. immaculicollis* there are eight setae on the dorsal aspect of each of first seven abdominal segments, but in *H. triopsis* there are only six setae.

KEY FOR THE IDENTIFICATION OF THE IMMATURE STAGES OF HALIPLIDAE DESCRIBED IN THIS PAPER

EGGS

Eggs laid singly *on* branches of aquatic plants; color yellow; over 0.4 mm. in length........ ....Genus *Peltodytes*

Eggs inserted singly *within* branches of aquatic plants; color white; under 0.4 mm. in length.......... ....Genus *Haliplus*

LARVAE

1 (14) Body with numerous elongated, segmented projections; abdomen nine-segmented..... ....Genus *Peltodytes* 2

2 (3) Projections two-segmented; mandibles with 2 setae on lateral aspect; antenna three-segmented.........FIRST LARVAL INSTAR (No specific difference among three species: *P. edentulus* Lec., *P. sexmaculatus* Rbts. and *P. lengi* Rbts.)

3 (2) Projections more than two-segmented; mandibles with more than two 2 setae on lateral aspect; antenna three-segmented or more..4

4 (9) Projections eight- or nine-segmented; mandibles with 3 setae on lateral aspect; antenna three-segmented. .. .. SECOND LARVAL INSTAR 5

5 (8) Length of spine on dorsal projections not greater than diameter of projection.................................... ...6

6 (7) Length of spine on dorsal projections equal to about two thirds of diameter of projections..................*P. edentulus* Lec.

7 (6) Length of spine on dorsal projections about equal to diameter of projections........ ....*P. lengi* Rbts.

8 (5) Length of spine on dorsal projections equal to about one and one-third times diameter of projections.......*P. sexmaculatus* Rbts.

9 (4) Projections twelve to eighteen-segmented; mandibles with 6 setae on lateral aspect; antenna four-segmented .... THIRD LARVAL INSTAR 10

10 (13) Length of spine on dorsal projections not greater than diameter of projections............ 11

11 (12) Length of spine on dorsal projections equal to about two thirds of diameter of projections..................*P. edentulus* Lec.

12 (11) Length of spine on dorsal projections about equal to diameter of projections...............................*P. lengi* Rbts.

13 (10) Length of spine on dorsal projections equal to about one and one-third times diameter of projections........*P. sexmaculatus* Rbts.

14 (1) Body with numerous setigerous tubercles; abdomen ten-segmented..............................Genus *Haliplus* 15

15 (20) Tibia of first thoracic legs with thumb-like prolongation on disto-ventral margin; adapted for grasping.....................16

16 (17) Dorsal aspect of each segment of body with few setigerous tubercles; 8–10 on each of the first seven abdominal segments..........FIRST LARVAL INSTAR, *H. immaculicollis* Harr.

17 (16) Dorsal aspect of each segment of body with several setigerous tubercles; 30–100 or more on each of the first seven abdominal segments..18

18 (19) Dorsal aspect of each segment of body with 30–35 setigerous tubercles on each of the first seven abdominal segments.... SECOND LARVAL INSTAR, *H. immaculicollis* Harr.

19 (18) Dorsal aspect of each segment of body with over 100 setigerous tubercles on each of the first seven abdominal segments.... THIRD LARVAL INSTAR, *H. immaculicollis* Harr.

20 (15) Tibia of first thoracic legs without thumb-like prolongation on disto-ventral margin; not adapted for grasping..............21

21 (24) Dorsal aspect of each segment of body with several setigerous tubercles; 10–20 on each of the first seven abdominal segments............................SECOND LARVAL INSTAR 22

22 (23) Dorsal aspect of each segment of body with four prominences bearing setigerous tubercles; 5–8 on each of the first seven abdominal segments..........................*H. triopsis* Say

23 (22) Dorsal aspect of each segment of body with four prominences bearing setigerous tubercles; 10–12 on each of the first seven abdominal segments.......................*H. cribrarius* Lec.

24 (21) Dorsal aspect of each segment of body with many setigerous tubercles; more than 60 on each of the first seven abdominal segments..........................THIRD LARVAL INSTAR 25

25 (26) Dorsal aspect of each segment of body without any horn-like projections...................................*H. triopsis* Say

26 (25) Dorsal aspect of each segment of body with four horn-like projections...............................*H. cribrarius* Lec.

PUPA

Setae unequal in length...............................Genus *Peltodytes*
Setae about equal in length...........................Genus *Haliplus*

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EXPLANATION OF PLATE XLVII

Peltodytes lengi Roberts

FIG 1. Egg attached to branch of Ceratophyllum

FIG. 2. Egg showing group of ocelli

FIG. 3. Micropyle

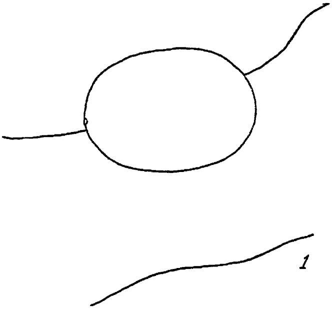
FIG. 4. Egg after hatching

FIG. 5. Right antenna of first larval instar, dorsal view

FIG. 6. Right mandible of first larval instar, dorsal view

FIG. 7. First larval instar, dorsal side (to the left) and ventral side (to the right)

PLATE XLVII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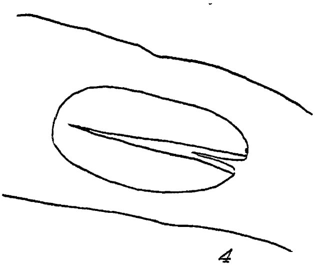
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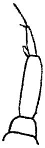
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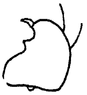
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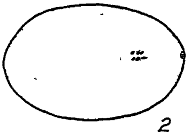
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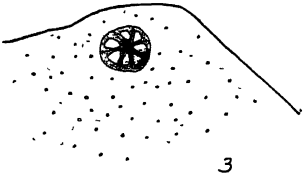
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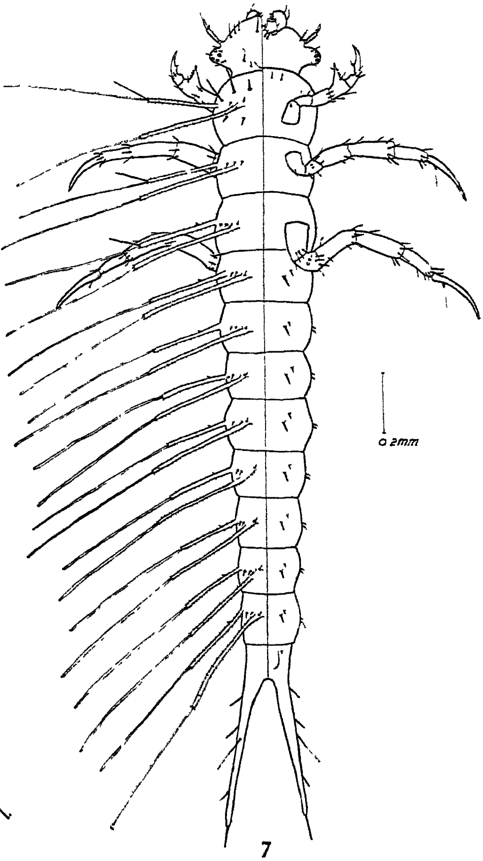


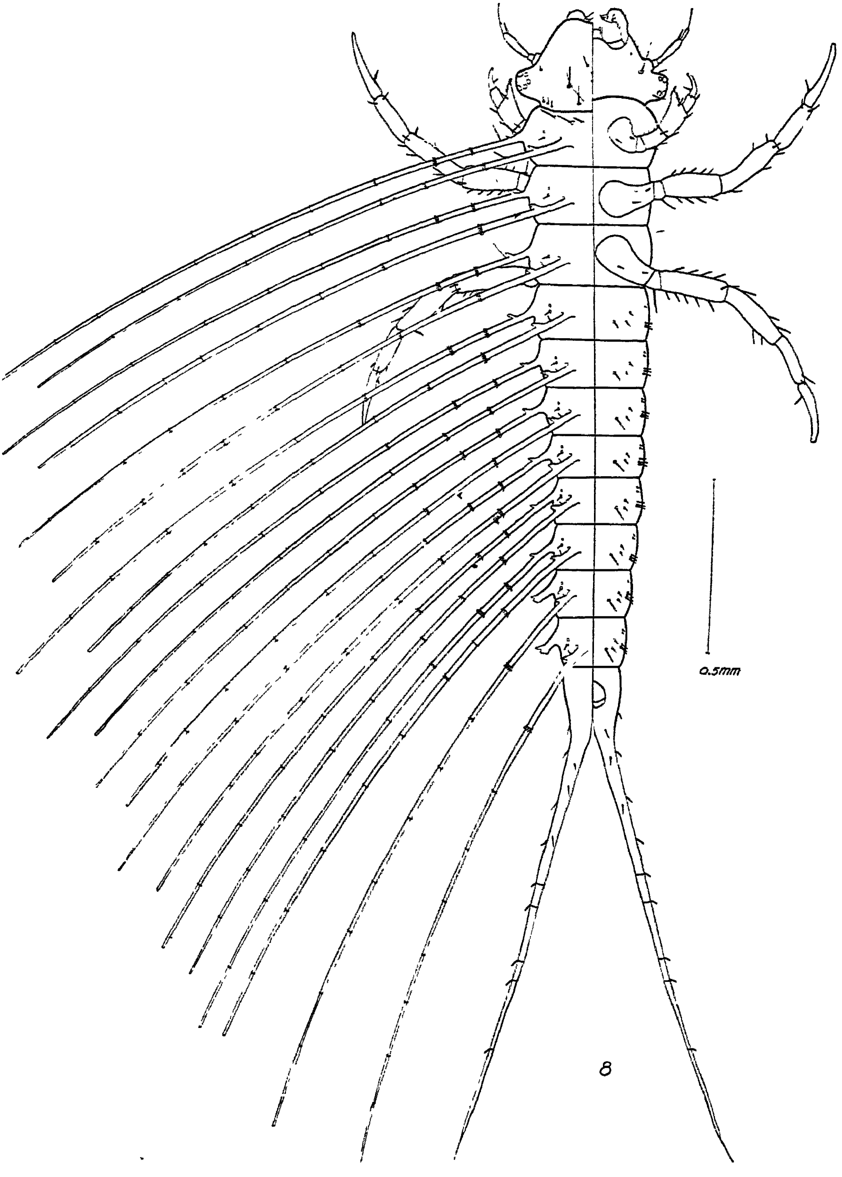
7

EXPLANATION OF PLATE XLVIII

Peltodytes lengi Roberts

FIG. 8. Second larval instar, dorsal side (to the left) and ventral side (to the right)

PLATE XLVIII

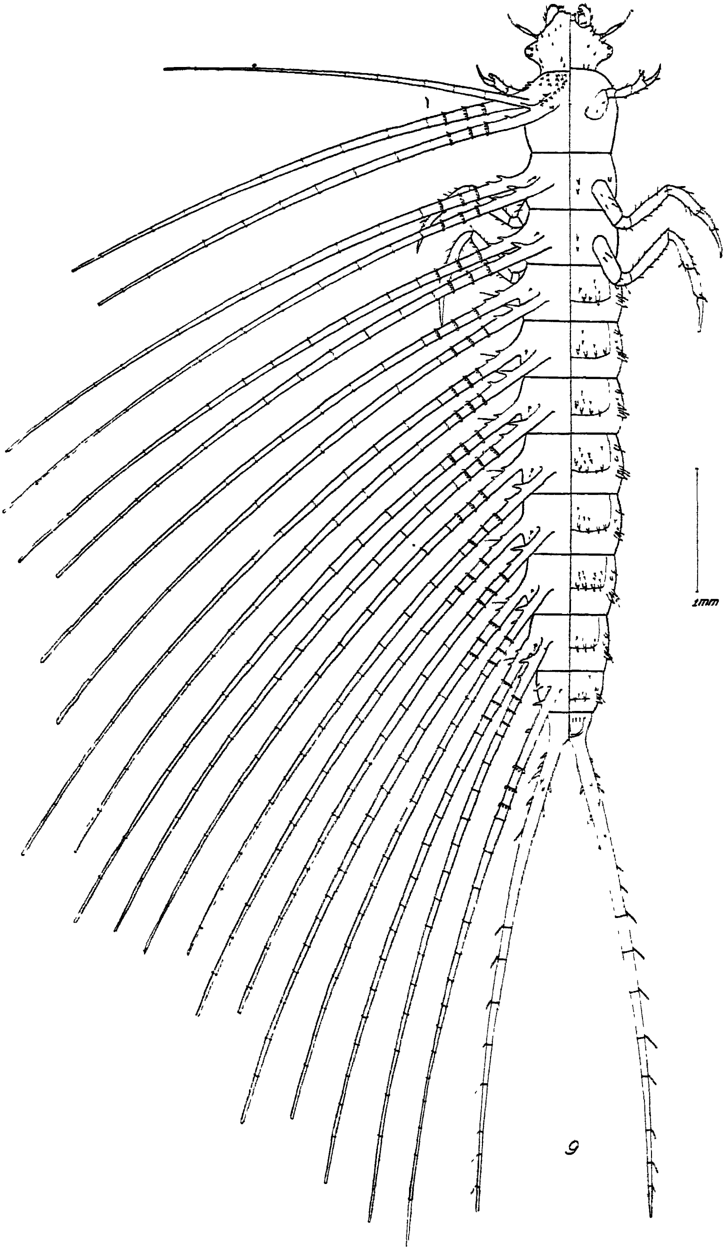


EXPLANATION OF PLATE XLIX

Peltodytes lengi Roberts

FIG. 9. Third larval instar, dorsal side (to the left) and ventral side (to the right)

PLATE XLIX



9

EXPLANATION OF PLATE L

Peltodytes lengi Roberts (except Figs. 18 and 20)

Third larval instar

FIG. 10. Head capsule of *P. lengi*, dorsal side (to the left) and ventral side (to the right)

FIG. 11. Head capsule of *P. lengi*, lateral view showing ocelli

FIG. 12. Right antenna of *P. lengi*, dorsal view

FIG. 13. Right and left mandibles of *P. lengi*, ventral view

FIG. 14. Right maxilla of *P. lengi*, ventral view

FIG. 15. Labium of *P. lengi*, ventral view

FIG. 16. First thoracic leg of *P. lengi*, right

FIG. 17. Prolongation of tibia, first thoracic leg of *P. lengi*, ventral view

FIG. 18. Spine on dorsal projection of *P. edentulus*

FIG. 19. Spine on dorsal projection of *P. lengi*

FIG. 20. Spine on dorsal projection of *P. sexmaculatus*

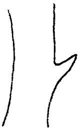
FIG. 21. Head capsule of *P. lengi* showing suction canal of mandibles

Pupa

FIG. 22. Pupa of *P. lengi*, ventral view

FIG. 23. Pupa of *P. lengi*, lateral view

PLATE L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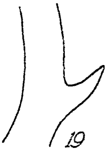
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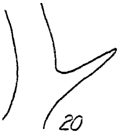
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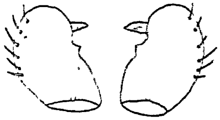
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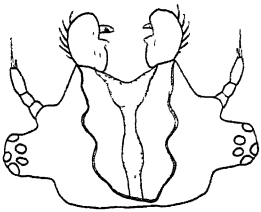
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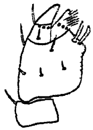
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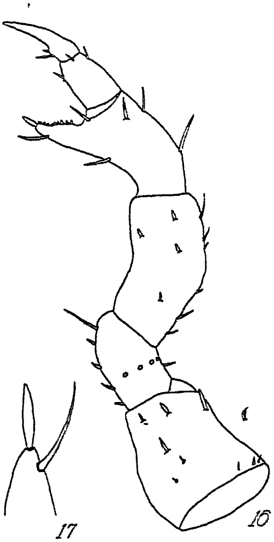
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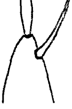
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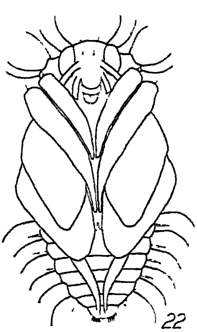
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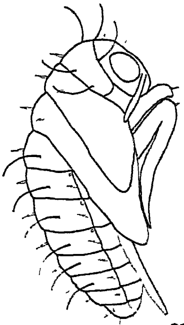
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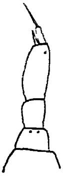
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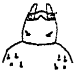
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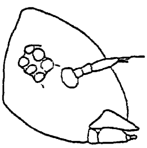
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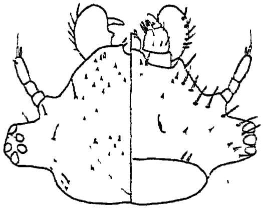
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EXPLANATION OF PLATE LI

Haliplus immaculicollis Harris

FIG. 24. Egg inserted in branch of Ceratophyllum

First larval instar

FIG. 25. First larval instar, dorsal side (to the left) and ventral side (to the right)

FIG. 26. Right antenna of first larval instar, dorsal view

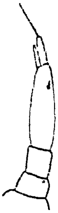
FIG. 27. Caudal segment of first larval instar, dorsal view

Second larval instar

FIG. 28. Second larval instar, dorsal side (to the left) and ventral side (to the right)

FIG. 29. Right antenna of second larval instar, dorsal view

PLATE LI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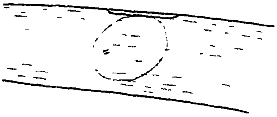
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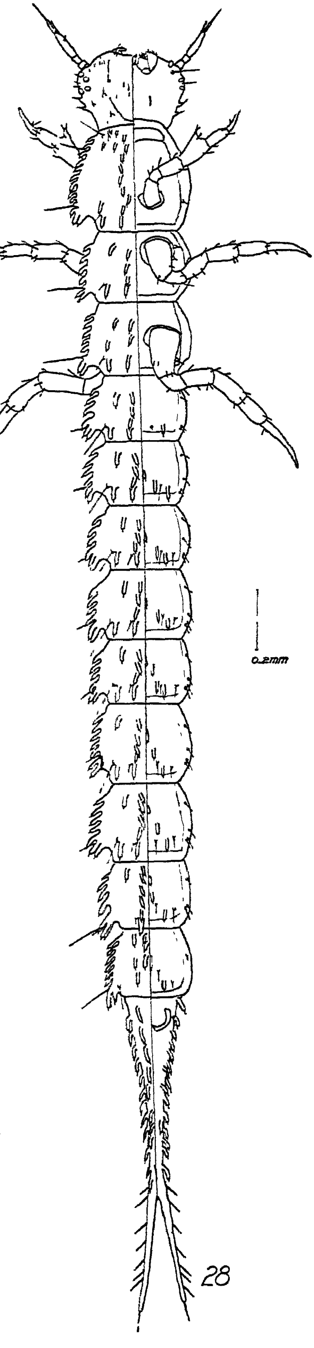

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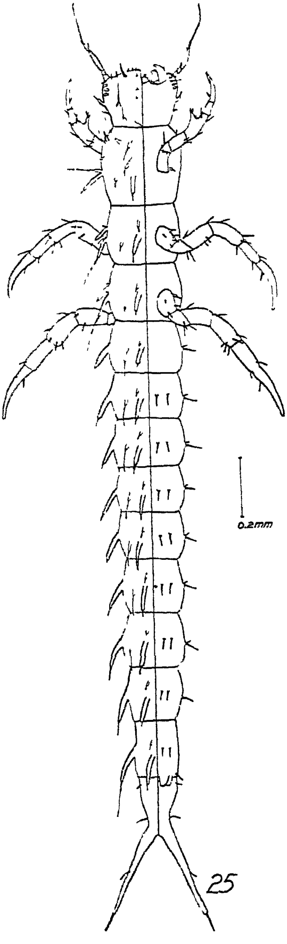

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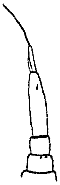
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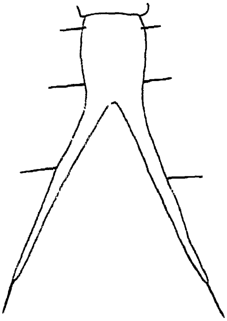
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EXPLANATION OF PLATE LII

Haliplus immaculicollis Harris

FIG. 30. Third larval instar, dorsal side (to the left) and ventral side (to the right)

FIG. 31. Head capsule of third larval instar, lateral view

FIG. 32. Left antenna of third larval instar, dorsal view

FIG. 33. Right mandible of third larval instar, ventral view

FIG. 34. Right maxilla of third larval instar, ventral view

FIG. 35. Labium, ventral view

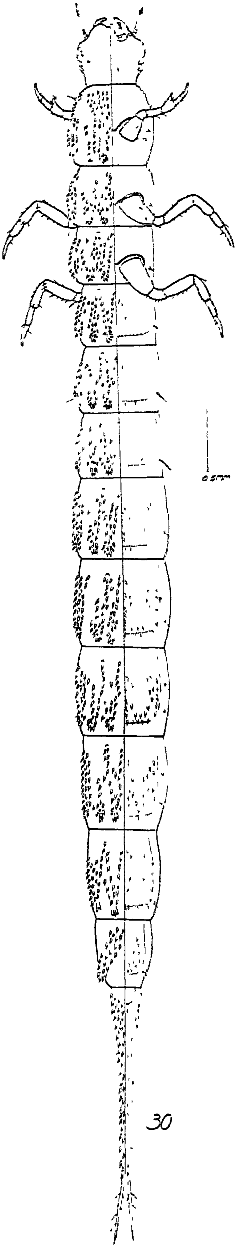
FIG. 36. Caudal segment of third larval instar, dorsal view

FIG. 37. First thoracic leg of third larval instar, right

FIG. 38. Prolongation of tibia, first thoracic leg, third larval instar, ventral view

FIG. 39. Pupa, dorsal view

PLATE LII



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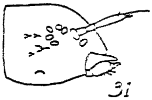

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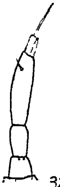

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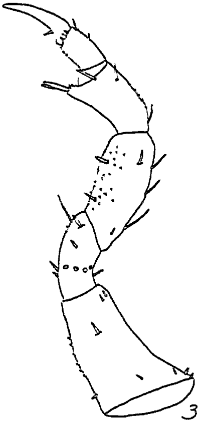

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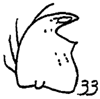

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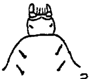

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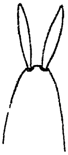

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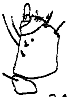

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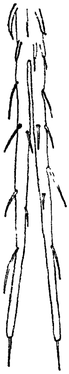

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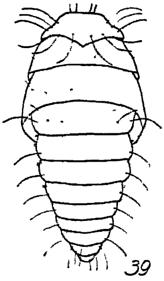


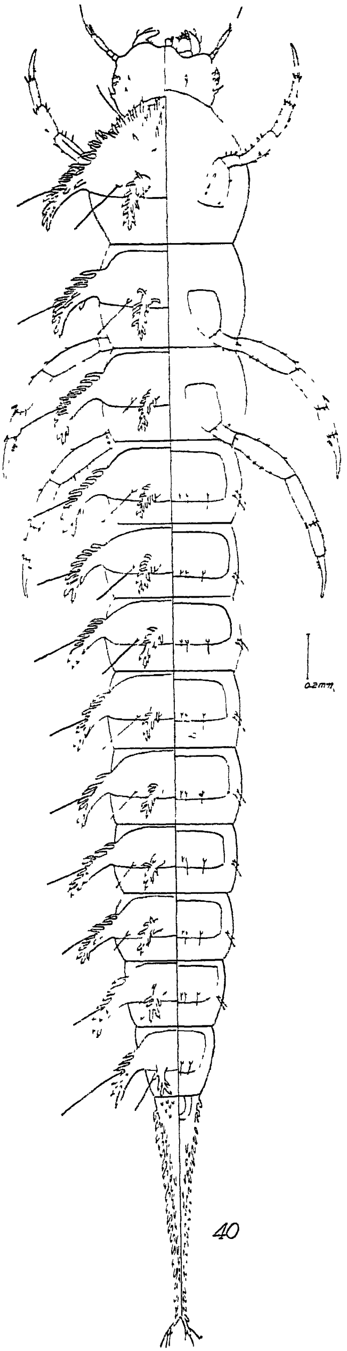
39

EXPLANATION OF PLATE LIII

FIG. 40. Second larval instar of *H. cribrarius*, dorsal side (to the left) and ventral side (to the right)

FIG. 41. Second larval instar of *H. triopsis*, dorsal side (to the left) and ventral side (to the right)

PLATE LIII



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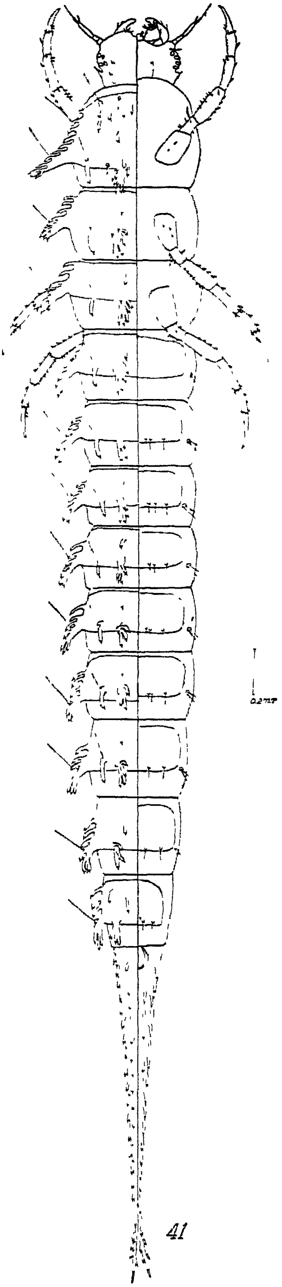

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EXPLANATION OF PLATE LIV

Haliplus cribrarius Le Conte

FIG. 42. Third larval instar, dorsal side (to the left) and ventral side (to the right)

FIG. 43. Head capsule of the third larval instar, dorsal side (to the left) and ventral side (to the right)

FIG. 44. Head capsule of third larval instar, lateral view

FIG. 45. Left antenna of third larval instar, dorsal view

FIG. 46. Right maxilla of third larval instar, ventral view

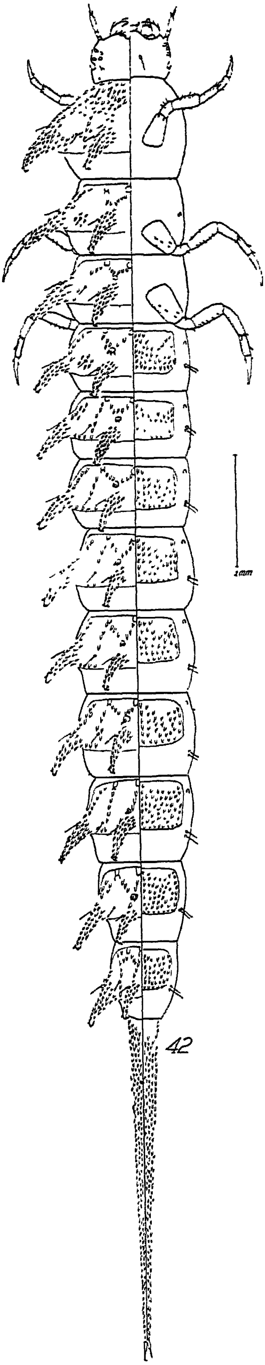
FIG. 47. Labium of third larval instar, ventral view

FIG. 48. Horn-like process of third larval instar, lateral view

FIG. 49. Terminal portion of caudal projection, third larval instar

FIG. 50. First thoracic leg of third larval instar, right

PLATE LIV



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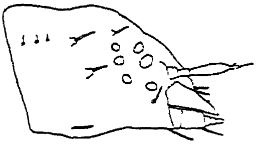

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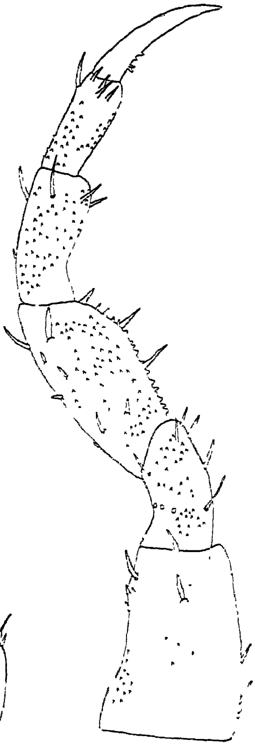

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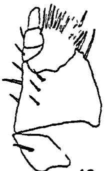

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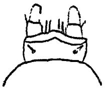

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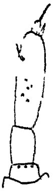

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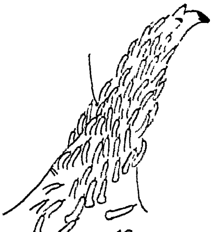

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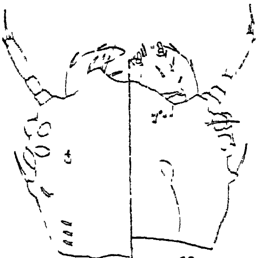

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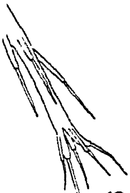

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EXPLANATION OF PLATE LV

Haliplus triopsis Say

FIG. 51. Third larval instar, dorsal side (to the left) and ventral side (to the right)

FIG. 52. Head capsule of third larval instar, dorsal side (to the left) and ventral side (to the right)

FIG. 53. Head capsule of third larval instar, lateral view

FIG. 54. Left antenna of third larval instar, dorsal view

FIG. 55. Right mandible of third larval instar, ventral view

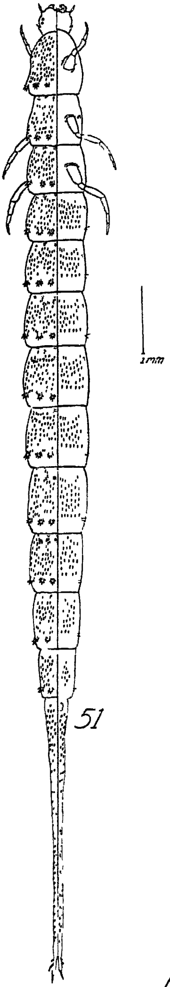
FIG. 56. Right maxilla of third larval instar, ventral view

FIG. 57. Labium of third larval instar, ventral view

FIG. 58. Terminal portion of caudal projection of third larval instar

FIG. 59. Third thoracic leg of the third larval instar, right

PLATE LV



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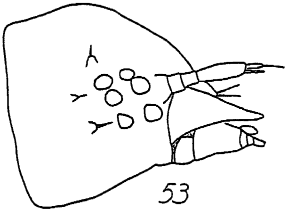

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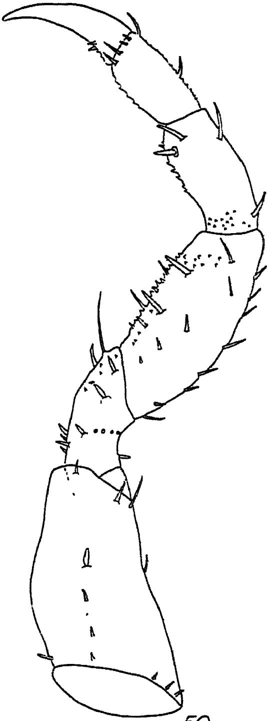

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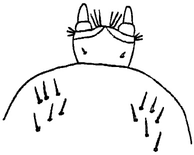

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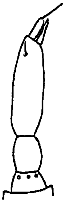

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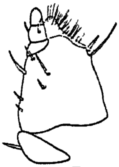

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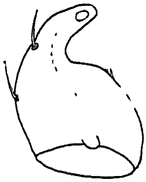

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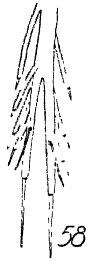

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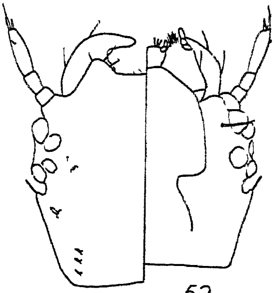

52

FURTHER ADDITIONS AND CORRECTIONS TO THE LIST OF THE FISHES OF THE GREAT LAKES AND TRIBUTARY WATERS

CARL L. HUBBS

IN 1926, I wrote that "the fish fauna of the Great Lakes and tributary waters comprises 28 families, 96 genera and 154 species, or, including also subspecies, a total of 166 forms. A few of these are perhaps erroneously accredited to the basin, and it may later be found impossible to recognize some of the subspecies here accepted. It is probable, also, that a few, but not many, additions to the list will be made in the future." I was a poor prophet, for only two years later (Hubbs and Greene, 1928) the list was increased to "158 species or a total of 180 forms, subspecies included." And now, after two more years, we have discovered that several additional species inhabit the Great Lakes drainage basin. Today the list stands as 28 families, 98 genera and 168 species, or a total of 192 forms, subspecies included. The figure last given represents an increase of 16 per cent over the corresponding one given in 1926. I will venture no further predictions in regard to future additions to the list.

1. Leucichthys reighardi dymondi Koelz

This northern race of *Leucichthys reighardi* has recently been differentiated by Koelz (1929 a, p. 406). It is the form listed by Hubbs and Greene (1928, p. 386) as a *nomen nudum*, under the manuscript name of *Leucicthys reighardi borealis* Koelz.

In the same paper by Koelz, *Leucichthys kiyi orientalis* and *Leucichthys nigripinnis regalis* are also described.

2. Leucichthys hubbsi Koelz

A small cisco from Ives Lake, northern Michigan, distinctly different from any of the Great Lakes species, has recently been described by Koelz (1929 b) as a new species.

3 a. Salmo gairdnerii irideus Gibbons
3 b. Salmo gairdnerii shasta Jordan

It seems clear, despite the contrary interpretation of Jordan (1923), that *Salmo gairdnerii* Richardson was based on the large, rather fine-scaled steelhead which runs up the Columbia River from the ocean. The square-cut shape of the tail, emphasized by Richardson, applies to no salmon. It is not clear that the high vertebral count was taken from the type, which was clearly the specimen described by Gairdner in a letter to Richardson, nor is it impossible that the fine-scaled steelhead may have as many as 66 vertebrae, counting all rudiments in the upturned axis at the end of the column.

The typical subspecies *gairdnerii*, as it has several times been observed, differs appreciably from the common coarse-scaled type of the small coastal streams of the Pacific Coast, *Salmo gairdnerii irideus*. The two forms, however, cannot be regarded as specifically distinct, on the species criterion of virtually complete differentiation (which I accept). The whole group of races comprising the rainbow or steelhead series, with the probable exception of the golden trout, are too alike and too overlapping in their characters to admit the view that any one is completely differentiated from the others.

4. Cristivomer namaycush huronicus Hubbs

A peculiar dwarfed race of lake trout, found in the deep waters of Rush Lake, northern Michigan, appears sufficiently differentiated from the typical form to warrant subspecific separation. A brief characterization has been given (Hubbs, 1929, p. 155) in *The Book of Huron Mountain;* it will later be discussed in an article in *Ecology*. The former account of the subspecies will have to be regarded as the type diagnosis, and is here quoted to make it more generally accessible:

> Of exceptional interest is the occurrence in Rush Lake of two kinds of lake trout. The ordinary type occurs in moderate depths in the summer, while the *Rush Lake trout* (*Cristivomer namaycush huronicus*) occupies the deep trough, which, though little more than one-fourth mile wide, descends to a depth of 270 feet. This deep water trout reaches a weight of about two pounds only, and matures when considerably smaller, at a size when the shallow water type is always immature. It also spawns earlier, in late summer rather than in the fall. So far as known, this interesting little trout occurs nowhere else.

The most noteworthy physical characteristics of the new form are the broadly U-shaped snout, as seen from above, the small mouth, and the lack of sexual dimorphism.

5. Megastomatobus cyprinella (Cuvier and Valenciennes)

The discovery of a specimen of this species in the Museum of Comparative Zoölogy, collected by Kirtland at Rockport, Ohio, shows that this species has at least sporadically occupied the Lake Erie watershed for many years.

6. Ictiobus niger (Rafinesque)

The black or mongrel buffalo has incorrectly been identified as *Ictiobus urus* (Agassiz), which I have found, by examining the types, to be a synonym of *I. bubalus*. The older name of Rafinesque, however, seems identifiable with the present form, for which I am proposing (Hubbs, 1930) that it be adopted.

This species occurs as far north in Lake Michigan as Black Lake, near Holland.

7. Ictiobus bubalus (Rafinesque)

That the razor-back buffalo is a species distinct from the preceding species can scarcely be doubted. My former uncertainty as to distinctness (Hubbs, 1926, p. 20) was due to my inexperience with the group. A comparison of the two species is being given elsewhere (Hubbs, 1930), along with a record of a specimen in the Museum of Comparative Zoölogy, taken long ago at Homer, Michigan, which is on the St. Joseph River. This record is the first for the Great Lakes drainage basin.

8. Carpiodes carpio (Rafinesque)

A specimen of this sucker has been collected in the Lake Erie drainage basin of Ohio by M. B. Trautman. It has not before been reported from the Great Lakes area.

9. Erimyzon sucetta kennerlii (Girard)

10a. Erimyzon oblongus oblongus (Mitchill)

10b. Erimyzon oblongus claviformis (Girard)

The genus *Erimyzon*, instead of comprising but one species and two imperfectly distinguished subspecies, is made up of three species, two of which are divisible into eastern and western subspecies. All these are differentiated and discussed in another paper (Hubbs, 1930).

11. Moxostoma duquesnii (Le Sueur)

12. Moxostoma rubreques Hubbs

13. Moxostoma erythrurum Rafinesque

These three species of "mullets" have been confounded by recent authors under the erroneously applied name, *Moxostoma aureolum* (Hubbs, 1930).

14. Moxostoma aureolum (Le Sueur)

It is elsewhere shown (Hubbs, 1930) that the name *aureolum* must be returned to the short-headed redhorse of the Great Lakes and northward, which is now known as *M. lesueurii.* The true *M. breviceps*, of the upper Ohio and Tennessee basins, is specifically distinct.

15. Hybopsis storerianus (Kirtland)

16. Hybopsis amblops (Rafinesque)

The generic name *Hybopsis* has had a vacillating history since its proposal by Agassiz in 1854. The genus was based on *Hybopsis gracilis* Agassiz, but when his paper was in press Agassiz in a footnote referred to the same genus another new species, *H. dorsalis*, which we have shown (Hubbs and Greene, 1928, p. 380) to be identical with *Notropis gilberti* Jordan and Meek. Cope used the name *Hybopsis* for what is now generally interpreted as a section of *Notropis*. Jordan and Evermann and others, however, regarded *Hybopsis gracilis* as a synonym of *Rutilus amblops* Rafinesque, and therefore used the generic name for a different genus having a barbel. Recently Jordan (1924, p. 51) reversed his former view, for he regarded *Hybopsis gracilis* as identical with the species called *Notropis blennius* by Jordan, and accepted the name *Hybopsis* for the *Alburnops* group of *Notropis*.

The species generally called *Notropis blennius*, which name, on this view of Jordan, would be replaced by *Hybopsis gracilis*, we have shown to be a complex of two species, *deliciosus* and *volucellus* (Hubbs and Greene, 1928, pp. 375–376). Of these, we have seen only *volucellus* from the vicinity of the southern bend of the Tennessee, the type region of *Hybopsis gracilis*. Agassiz we may assume did not have *volucellus*, because he expressly states that the anal fin has seven rays. This number often occurs in the species called *Hybopsis amblops* by Jordan and Evermann. A careful reading of the type description of *H. gracilis* gives one the clear impression that Agassiz had *Hybopsis amblops* before him. The large superior eye and "obtuse prominent" snout, emphasized by Agassiz, are especially characteristic of *amblops*. That he really had that species is virtually assured by the examination of a colored sketch of the type made by Burkhardt for Agassiz in February, 1854, when the specimen was fresh. This picture, kindly loaned me by Dr. Barbour, shows a fish with the general body and head form of *amblops;* a large superior eye; heavy projecting snout; yellowish color with a silvery band; the underlying dark band not evident on body except near caudal base (as would be expected on an alcoholic specimen), but appearing across opercle, and on the side of the snout, where it is directed obliquely downward and forward as typically in *amblops*.

I conclude that *Hybopsis gracilis* should be re-identified with the genus and species called *Hybopsis amblops* by Jordan and Evermann, but recently assigned the later generic and specific name *Erinemus hyalinus*. The application of the specific name *amblops* is, I believe, also justified, for Rafinesque emphasized the prominent blunt snout and large eye, the two characters of the species which would most probably impress the keen but uncritical Rafinesque. The present species I therefore call, with Jordan and Evermann, *Hybopsis amblops.* Provisionally, the species *storerianus* should be retained in the same genus.

17. Rhinichthys atronasus meleagris Agassiz

A recent study of the types of *Rhinichthys meleagris* Agassiz, in the Museum of Comparative Zoölogy, shows, as we have long suspected, that this name was based on the subspecies currently known as *Rhinichthys atronasus lunatus.* Since Agassiz's name has priority over that of Cope's, it must be used. Some discussion of the relationship between subspecies *meleagris* and *atronasus* is given by Hubbs and Brown (1929, p. 25).

18. Notropis dorsalis dorsalis (Agassiz)

Hubbs and Greene (1928, pp. 380–381) have shown that the name *Notropis dorsalis* must replace that of *N. gilberti.* Recent study of specimens in the zoölogical museums of Harvard and Michigan has shown that this form intergrades with *Notropis piptolepis* (Cope) in eastern Nebraska. Trinomial nomenclature is therefore in order.

19. Notropis rubellus (Agassiz)

Hubbs and Brown (1929, p. 34) have shown, in the account here quoted, that without question *Photogenis rubrifrons* Cope is a synonym of *Alburnus rubellus* Agassiz.

> This name, the oldest for the species, has generally been treated as synonymous with *N. atherinoides*, and we have even stated (Hubbs and Green, 1928, p. 381) that the type of *rubellus*, on reëxamination, has proved identical with *Notropis atherinoides.* The specimen in question, however, cannot be regarded as the type, as the result of a more complete study of the Museum of Comparative Zoology collections. It is a bleached example that had been on exhibition, after having been removed from lot number 1749, labelled "Sault St. Mary and the Pic." These are the localities mentioned in the type description (Agassiz, 1850, pp. 364–366, pl. 3, fig. 1–3): "The species is very common at the Sault of St. Mary; specimens were also obtained at the Pic."
>
> The fourteen specimens remaining in this compound lot comprise 5 of *rubrifrons* and 9 of *atherinoides.* In all probability the specimens from "the Pic" are *atherinoides*, while those from the Sault are *rubrifrons.* The actual type locality is Sault Ste. Marie, by reason of Agassiz's wording quoted above,

and, if necessary, by present designation. Therefore, the name *rubellus* should replace *rubrifrons* rather than be synonymized with *atherinoides*.

A careful reading of Agassiz's original description makes it clear, in fact. that his account of *rubellus* was based on *rubrifrons* rather than on *atherinoides*, When items of possible distinguishing value appear, the description fits *rubrifrons* the better. We quote the most pertinent statements — ". . . its form is elegant, slender, the back somewhat more convex than the belly; the tail is contracted. The greatest height of the body corresponds to the anterior third, or the region situated between the pectorals and the ventrals, and is contained six times in the length, exclusive of the caudal fin. The head, small, conical and compressed, like the sides, is somewhat less than the fifth of the total length . . . the eyes are large and circular [this one statement applies the better to *atherinoides*, but is more than counterbalanced by what immediately follows], approaching the upper region of the head, and at an equal distance from the end of the snout and the posterior extremity of the opercular apparatus. . . . There are some reddish spots on the face and the opercular apparatus, fading sometimes into a uniform reddish tint all over the head and shoulders." Clearly the name *rubellus* can not be considered synonymous with *atherinoides*.

The specimen figured and probably the one described, certainly a *rubrifrons*, is fortunately recognizable individually by the actually abnormally arched front, low mouth and projecting lower jaw (the last point is mentioned in the description); it is the only specimen in the series that is tintagged, and is regarded by us as the holotype.

20. Hypargyrus velox Girard

That this species, usually known as *Cliola* or *Ceratichthys vigilax*, needs another name is indicated by Hubbs and Ortenburger (1929, p. 36), who show that the name *Ceratichthys vigilax* belongs with the genus and species usually known as *Cochlognathus ornatus*.

Hypargyrus velox has recently been recorded from the Great Lakes drainage basin of Wisconsin by Cahn (1928, p. 37). Other specimens have been taken by M. B. Trautman in Lake St. Marys, Ohio, which drains into Lake Erie as well as into the Ohio.

21. Pelodictis limosus Rafinesque

This name, which has priority over *Leptops* or *Opladelus olivaris* for the yellow cat, and has been adopted by some authors, I believe to be available and applicable. The description given by Rafinesque applies so well that the account cannot be interpreted as "imaginary." The greatest untruthfulness in the description is the statement that the second dorsal has rays, but the relatively immense adipose of this species would more probably be so described than that of any other North American siluroid.

If the name *Pelodictis limosus* should be regarded as unusable, then *Opladelus olivaris* would be in order. *Opladelus* and *Leptops* are of identical date, but Gill, the first reviser, chose the former, as Jordan (1929, p. 92) has recently recalled.

22. Schilbeodes furiosus (Jordan and Jenkins)

This species of "mad tom" is currently listed as occurring only in the Tar and Neuse river systems of North Carolina. But we have specimens from the Ohio River drainage basin of Indiana and Ohio (those from Ohio were kindly sent me for study by E. L. Wickliff and M. B. Trautman). Another specimen, collected years ago in the Huron River at Ann Arbor, Michigan, gives us a Great Lakes record for the species. The western specimens agree well with North Carolina ones, examined in the National Museum.

Schilbeodes furiosus is supposed to differ from *S. miurus* in the much longer pectoral spine, which is said to be contained 1.25 times in the head. This descriptive feature, however, is based on the type, which is a selected variant from a series in which the spine is contained 1.2 to 1.6 times in the head (this series was examined at the National Museum). The spine, it is true, does average longer than in *S. miurus*. *S. furiosus* differs further from that species in having the procurrent caudal rays little developed, the notch between adipose and caudal deeper and sharper, and the distance from this notch to end of caudal more instead of less than two thirds of the distance from notch to origin of dorsal.

In these respects *S. furiosus* resembles *S. eleutherus*, with which it is occasionally taken in Indiana and Ohio. From that species it differs in the narrower and less depressed head, less swollen upper lip, much stronger pectoral spines. *S. furiosus* differs from both *miurus* and *eleutherus* in coloration. It is less mottled than *miurus* but more boldly marked than *eleutherus*. A feature highly diagnostic of *furiosus* is that the dorsal saddles are abruptly truncated and connected with one another below by a dark strand, so that the light background of the dorsal region is circumscribed into fairly distinct ovals.

23. Anguilla bostoniensis (Le Sueur)

Since the action of the first reviser is again regarded as overruling mere page or line priority, we should revert to the name *bostoniensis* for the American eel. This course has been suggested by Jordan (1929, p. 56), and I stand in agreement with him.

24. Percina caprodes semifasciata (De Kay)

Concerning the name, which apparently should replace that of *P. c. zebra* for the northern subspecies of *Percina caprodes,* I quote the statements of Hubbs and Brown (1929, p. 47):

> We have made a rather strained effort (Hubbs, 1926, p. 61, and Hubbs and Greene, 1928, p. 382) to hold on to the name *zebra* for the northern log perch, despite the fact that *Pileoma semifasciata* De Kay was described earlier from a northern locality. The Lake Champlain specimens previously examined, all from the Vermont side, were mostly of the *zebra* type, but a few showed a transition to typical *caprodes*. But after a more extended study of Lake Champlain material, in the Museum of Comparative Zoology, we find that examples from near the type-locality, on the New York side, are almost uniformly of the northern type. There appears, therefore, to be no way to avoid the necessity of changing the name of the northern subspecies of *Percina caprodes* to *P. c. semifasciata.*

25. Cottogaster copelandi Jordan

The account of the darters related to *Cottogaster* given by Hubbs and Greene (1928, pp. 382–384) involves some very serious errors of observation and judgment. These errors arose from the fact that both *Cottogaster copelandi* and *Imostoma shumardi* were represented in our collections from the lower Au Sable River, Michigan, but were not separated. Therefore some characters of *Imostoma,* particularly those of the breeding male, were assigned to *Cottogaster*. It is certain that *Rheocrypta* is a synonym of *Cottogaster*, and I can find no really satisfactory basis for the specific or even subspecific distinction of *C. putnami* from *C. copelandi*. There does appear to be a slight tendency toward more scales, a slenderer body, a more prominent snout and more tessellated markings toward the southwest, but none of the differences are trenchant, and at present I am at a loss to know where to draw the line between the ranges of the two forms. In most other respects the account by Hubbs and Greene, referred to above, appears sound.

The statement that "in some specimens from the Au Sable the premaxillaries are bound back by a frenum" (Hubbs, 1926, p. 61) is also an error. The specimens which appear to show the frenum are examples of *Imostoma shumardi,* which is generally wrongly recorded as showing such a variation. In that species, as also in *Ammocrypta pellucida* (see Hubbs, 1926, p. 62), the premaxillary groove is very shallow where it crosses the mid-line over the narrow premaxillary-forehead connection, which appears to be a true frenum in specimens which have died with the mouth open. When the mouth is closed, however, the cross furrow appears. In mouth structure *Imostoma* is really more like *Hadropterus* than *Cottogaster,* for in *Hadropterus* a slight crease is formed across the frenum when the mouth is tightly shut.

26. Imostoma shumardi (Girard)

The real characteristics and relationships of *Imostoma shumardi,* as just suggested, are inadequately indicated in the literature. I give, therefore, a revision of section c [1] of my 1926 key [1] (pp. 55–57).

c^1. — Mid-line of belly with a single series of scales, which are more or less enlarged, thickened, spinous, caducous and separated from adjacent scales by a groove on either side (these scales only incipiently modified in *Imostoma* and sometimes scarcely specialized in *Hadropterus phoxocephalus*). Pelvic fins separated by an interspace at least three fourths as wide as base of fin. Anal fin usually almost as large as second dorsal, or even larger. Body in most species elongate and little compressed. Vertebrae 37 to 44.

  d^1. — Flesh opaque. Anal spines 2. Squamation more nearly complete. Body less extremely elongate (depth 5.0 to 7.0).

    e^1. — Premaxillaries scarcely protractile, bound to snout by a fleshy frenum (which, however, is crossed by a shallow groove, quite well developed in *Imostoma,* when the mouth is tightly closed). Air-bladder rather large, but thin-walled (well developed in young).

      f^1. — Snout not extended so far forward as the premaxillaries. Mouth more or less oblique. Anal spines stiff.

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[1] In the same key, under h [1] and h [2], "premaxillaries" was inadvertently written when "maxillaries" was intended.

Skull distinctly less depressed, and narrower between the eyes (interorbital width 5.5 to 8.0). Scales of moderate size (fewer than 80). Color pattern consisting essentially of broad bars or horizontally elongated blotches (slightly approaching that of *Percina* in *Imostoma* and in *Hadropterus nigrofasciatus*). Dorsal fins slightly to widely separated. Vertebrae 39 to 42.

g^1. — Belly mostly scaleless medially, but crossed before the anus by a bridge of scales, which are only very slightly modified and not enlarged along the mid-line. Premaxillary frenum usually hidden by the cross furrow behind premaxillary. Anal fin greatly enlarged and strongly tuberculated in breeding males..............*Imostoma*

g^2. — Belly mostly scaled, and with scales of the mid-line strongly modified, as described under c^1 (except sometimes in *phoxocephalus*). Premaxillary frenum usually not hidden by cross furrow. Anal fin not much enlarged, and (except in *H. evides*) not tuberculated in breeding males..... *Hadropterus*

f^2. — Snout extended forward as a small conical projection beyond the premaxillaries. Mouth horizontal. Anal spines very flexible. Skull more depressed, and broader between the eyes (interorbital width 4.0 to 5.0 in head). Scales small (78 to 103). Color pattern consisting essentially of zebra-like markings. Dorsal fins scarcely or not at all separated. Vertebrae 44........*Percina*

e^2. — Premaxillaries distinctly protractile, followed by a deep groove. Air-bladder rudimentary. Snout slightly projecting beyond premaxillaries. Mouth horizontal. Anal spines moderately flexible. Skull, scales and color pattern as in f^1. Vertebrae 38.............................*Cottogaster*

d^2. — Flesh pellucid. Anal spine single. Scales on trunk confined to sides of body. Body very elongate (depth 7.8 to 9.0). Premaxillaries protractile (but the groove shallow).....*Ammocrypta*

Clearly *Imostoma* is out of place as a subgenus of *Cottogaster*. If not valid, it should be united with *Hadropterus*, with which it has much more in common.

27. Allotis humilis (Girard)

The orange-spotted sunfish has not been recorded as ranging northeastward beyond Illinois, but we have specimens from Indiana, collected by H. R. Becker. It has been traced by E. L. Wickliff and M. B. Trautman even as far eastward as Lake St. Marys, Ohio. Since this lake has an outlet toward Lake Erie as well as toward the Ohio, the species must be added to the list of the fishes of the Great Lakes and tributary waters.

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FURTHER DISTINCTIONS BETWEEN *BUFO AMERICANUS* HOLBROOK AND *BUFO FOWLERI* GARMAN *

M. GRAHAM NETTING

NEARLY every herpetologist in the eastern United States has been forced to work out a set of characters for the separation of specimens of *Bufo americanus* and *B. fowleri* (from his own locality). Some of these criteria have been published, and have proved of distinct value in restricted areas. However, the only recent definition of the two species, which applies throughout their ranges, is that by Myers (5).

The present study was undertaken for the purpose of determining the diagnostic value of the characters which are generally used to distinguish these species, and in the hope that additional ones might be found. The results are presented, not as final dicta, but merely as a series of suggestions to students who may have to deal with the same problem in the future. Admittedly, the number of specimens examined (210 of *fowleri*, and 60 of *americanus*) is small, compared to the numbers available, but, according to the principle of random sampling, the statistical results should serve as a reliable index to the results to be derived from the study of larger series. Most of the specimens upon which this report is based are in the Museum of Zoölogy of the University of Michigan. Only a small number of specimens of *americanus*, from various parts of its range, were examined, since this species is fairly well understood. Specimens of *fowleri* from the following states were studied: Alabama, Connecticut, Illinois, Indiana, Kentucky, Louisiana, Maryland, Massachusetts, Michigan, Mississippi, Missouri, New York, North Carolina, Tennessee, Texas and Virginia. The writer has studied *fowleri*, in the field, in New Jersey,

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* Contribution from the Museum of Zoölogy of the University of Michigan.

New York and Pennsylvania, as well; and has collected *americanus* in many states. From twenty to twenty-five measurements and observations were taken on each of the two hundred and seventy specimens. Most of the characters examined are discussed in detail below.

Bufo fowleri is considerably smaller than *americanus.* The average head-body length (snout to vent) is 58.6 mm. for 89 male *fowleri,* 59.9 mm. for 55 female *fowleri,* and 83.3 mm. for 17 female *americanus.* The largest males of *fowleri* which I have seen are 65 mm. in length. A female *fowleri* from Missouri measures 78.5 mm., and a female *americanus* from Michigan reaches 107 mm. Western specimens of *fowleri* average several millimeters longer than eastern specimens.

The lengths of the femur and tibia (= tibio-fibula) were taken for each specimen, in spite of the fact that the state of preservation frequently prevented uniform flexing of the legs. These measurements vary so much, even on similarly preserved specimens, that they cannot be used for diagnostic purposes. I agree with Miller and Chapin (4, p. 316), who have reported that they could not find any appreciable average difference in the leg measurements of the two species.

The head length and head width proved to be sufficiently constant for use, but no significant differences could be found between the species in the relationship of these measurements to head-body length, or to each other. As for the number of times that the head length of *fowleri* is contained in the head-body length, my figure closely approximates that of Ruthven (7, p. 4) rather than those of Dickerson (2, pp. 45, 94).

The size and shape of the parotoid gland proved to be of great diagnostic value. The parotoids of *fowleri* are elongate-oval, rather low and rarely descending on the neck posteriorly, whereas the glands of *americanus* are kidney-shaped or irregular in outline, high and frequently descending posteriorly. In 200 specimens of *fowleri* the parotoid averages 2.1 times as long as wide, but in 50 specimens of *americanus* the average is only 1.8 times as long as wide. These averages show even greater diversity when the measurements of adult specimens only are used. Furthermore, in *fowleri* the anterior tip of the parotoid is usually in contact with the transverse portion of the postorbital ridge; in *americanus,* it is separated from this ridge by a distance of a millimeter or more.

The character of the cranial crests varies greatly in both species. Only 44 per cent of 178 specimens of *fowleri* have parallel crests, although, in general, they are less divergent than in *americanus,* and show a greater tendency to slant upward toward the posterior ends. In southern specimens this gradual elevation approaches the condition in *terrestris,* though the terminal knobs are absent in *fowleri.* The top of the head is frequently raised to form a plateau between the cranial crests in *fowleri.* This plateau ends, more or less abruptly, on the line joining the postorbital ridges. This character sometimes makes it difficult to measure the height of the cranial crests. It seems to occur at random throughout the range of *fowleri,* and I have been unable to correlate it with any region or environment. In *americanus* the crests tend to be broader and more uniform in height, and in old specimens they may become parallel by a broadening toward each other at their posterior ends.

The number of warts to a dorsal spot is one of the most useful characters for separating the species. I wish, however, to amend the statements of previous writers by noting that *americanus* has one or *two* warts to a spot, while *fowleri* has more than two. One of the most reliable structural differences is the size of the warts on the upper surfaces of the hind legs, primarily in the femoral region. In *americanus* these warts are invariably greatly enlarged and irregular in size, but in *fowleri,* with the exception of some western specimens, they are not noticeably enlarged. This character is so constant, over most of the range, that it serves to distinguish even young specimens almost instantly. Conversely, specimens of *fowleri* have one row of large, and sometimes a secondary row of small, light-colored warts on the posterior surface of the forearm. In *americanus* the warts in the same region are generally uniform in size, not placed in a distinct row, and similar in color to the other warts on the arm.

Ruthven, Thompson and Gaige (8, pp. 33, 36) describe the subarticular tubercles of the fourth toe as double in *americanus* and single in *fowleri*. If limited to the second tubercle in *fowleri*, this distinction holds good throughout the range of the species. In all the specimens of *fowleri* which I have examined, the second tubercle is single; in 52 specimens of *americanus* it is double in 62 per cent. In eastern *fowleri* the first tubercle is rarely divided, in western specimens it is frequently divided, and in *americanus* it is generally double.

Spinosity is more characteristic of *americanus* than of *fowleri*. In any locality the former appears to have more spines, and much larger and heavier spines, than the latter. The dorsal surface of *fowleri* is rarely smooth, and if the specimens are examined carefully, the tiny spines on the warts can be seen readily. The ventral areolae are often smooth, but in many specimens tiny, horny pustules can be seen under a hand lens, and in Missouri specimens these are visible without a lens. It must be remembered that the visibility of these pustules depends upon preservation, for even flabby *americanus* may seem quite smooth.

The projecting muzzle of *fowleri* is a fairly reliable character, if used by a worker who is familiar with the two species. It cannot be depended upon for popular use, however.

There are certain types of marking and coloration which occur throughout the North American bufonids. In many specimens I believe that these are associated with the customary habitat of each species, and may be expected to vary wherever the form occurs in a different habitat in some other portion of its range. Thus the typical eastern *fowleri* inhabit sand beaches, and they display pronounced counter-shading. Sharply defined markings of light and dark are associated with a region of brilliant light and hard shadows. The vertebral stripe is distinct; the belly is immaculate; the lateral light and dark markings are arranged in clear stripes; and the dark bars on the hind legs are distinct. Missouri specimens, on the other hand, which occur on a darker background, presumably dirty river beaches and flood-plains, show less contrast in their markings. The vertebral stripe is indistinct; the belly is frequently dark-spotted; the lateral stripes tend to be broken up into mottlings; and the bars on the hind legs are only slightly more distinct than in *americanus*. Michigan specimens, and others from the beaches and dunes of the Great Lakes, are marked like Atlantic Coast specimens, as Hubbs (3, p. 43) has noted. Specimens from wooded and river-beach areas in Pennsylvania resemble the dun-colored Missouri specimens in coloring.

A light vertebral stripe is regularly present in *fowleri,* and frequently present in *americanus*. The character of this stripe is of greater diagnostic importance than its presence or absence. In *fowleri* it is narrow, well-defined, and of uniform width throughout its length; in *americanus,* when present, it is broader and highly irregular in width.

The dark bars on the upper surfaces of the hind legs are distinct in *fowleri,* and obscure in *americanus*. In the entire series of *fowleri* 195, or 92 per cent, show these markings very plainly.

Practically all *fowleri* have a dark breast spot. Of 210 specimens 80 per cent have no other markings ventrally (throat region excepted). Ventral spotting, however, is more common in western specimens than these figures would indicate. Thus of 58 eastern specimens 100 per cent are immaculate below; of 60 Tennessee specimens only 48 per cent are unspotted ventrally. I feel that this character is one of the least dependable of all those in common use for separating the two species. I consider that ventral spotting is associated with certain environments, and not with regions.

I have noted one character which may help to distinguish fresh material. In *americanus* there are commonly two or more slightly enlarged warts above the anal opening. In the small series of live material which I have examined for this character, these warts range in color from light orange to red. Many preserved specimens indicate clearly that these warts were more warmly colored than those below the anal opening. In *fowleri,* on the other hand, the warts in the same region are smaller, and either of the same color as those below, or darker.

Though I hesitate to make a statement before I have examined a series of fresh specimens, I suspect that the black throat of male *fowleri* is persistent throughout the year, and that male *americanus* are dark-throated only during the breeding season.

Ruthven (7, p. 4) and Allard (1, p. 464) have pointed out that the color of the iris cannot be used to separate the two species. The general color of *fowleri* is yellowish-gray or greenish-gray, but I have seen many dark specimens, and I judge that the red specimen listed by Myers (5, pp. 52–53) was not a "hybrid," but true *fowleri*.

Many writers have suggested that *fowleri* may interbreed with *americanus*, and Pickens (6, p. 109) has reported an "intermediate" between *fowleri* and *terrestris*. The first of these possibilities, at least, I regard as unlikely. Miller and Chapin (4, p. 317) cite the case of a male *americanus* clasping a female *Rana palustris* as an argument in favor of the possibility of interbreeding. I cannot see that this observation is pertinent to the question at issue. Nearly every herpetologist could cite dozens of cases of extra-specific clasping, and even cases of frogs clasping salamanders and fish, in the laboratory. Frequent attempts have been made to assign individual specimens to one of the two species by the use of insufficient, or highly variable, characters. When definite identification could not be made, the specimens were called "intermediates." Quite probably they were intermediate on the basis of the characters used. The confusion has arisen in the laboratory, however. If the two species do intergrade, is it not likely that specimens intermediate in behavior would have been recorded? I am well aware of the fact that the calls may vary somewhat, but I have never seen a specimen of either species which I could not easily identify by either call or behavior in the field, although I must admit that some of these specimens were hard to distinguish in the laboratory at a later date. Furthermore, *americanus* breeds from two to six weeks earlier than *fowleri*, and, as various writers have stated, it chooses different breeding grounds in many regions. Also, if intergrades occur, I should expect to find female *fowleri* which approach female *americanus* in size.

I believe that, according to Jordan's law, *americanus* and *fowleri* represent different lines of descent, but that in similar habitats the coloration of the two species develops in a parallel manner. All the structural differences which I have been able to observe tend to confirm the supposition that the species are more closely related to some other North American forms than to each other. I have refrained from discussing specimens of *fowleri* from the southern and western borders of its range, since I do not feel competent to discuss the variations in these regions before I have studied *terrestris* and the other species which complicate the problem.

A thorough study of the American forms of the genus *Bufo* would provide a fascinating problem in geographical distribution and genetic relationships for any investigator. The writer feels that an adequate analysis of such a complex group of species must be based upon statistical data derived from large series of breeding specimens, and supplemented by prolonged field-studies, and breeding experiments. Undoubtedly, some workers will regret the application of statistical methods in the field of herpetology. In cases similar to the one considered in this paper, however, in which the ranges of the species embrace widely different facies, and in which the diagnostic characters are highly variable, such methods are not only desirable, but well-nigh imperative. Until such a study is made the relationships of the American species of *Bufo* will remain undetermined.

The writer wishes to acknowledge his indebtedness to Dr. Alexander G. Ruthven, to Dr. Remington Kellogg and to Mrs. Helen T. Gaige for helpful criticism and advice.

University of Michigan

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ANATOMICAL DIFFERENCES IN THE SEXES OF THE MUSK TURTLE, *STERNOTHERUS ODORATUS* (LATREILLE) *

PAUL L. RISLEY

INTRODUCTION

CERTAIN characters which may be used in the identification of sex in turtles have been recognized and utilized by herpetologists for a long time. References to sex characters have seldom appeared in the literature touching upon the Chelonia. In the relatively few papers in which sex differences are recorded, actual data are not presented. A mere statement of the character in which the sexes supposedly differ is apparently considered adequate in itself. The records themselves are hidden in obscure papers which are primarily concerned with an entirely different problem. For this reason, the anatomist or embryologist who wishes to distinguish the sex of a chelonian from its external characters must depend upon his own observations and dissections.

In this investigation, I have made a study of various anatomical characters which may be used in the identification of sex in the common musk turtle, *Sternotherus odoratus* (Latreille). I shall attempt to show also, by a review of the literature on the subject, that there is reason to believe that some sex-identifying criterion will be found in every species of chelonian.

I wish here to express my appreciation and thanks to Dr. Peter Okkelberg of the Department of Zoölogy of the University of Michigan and to Dr. Carl O. Hubbs of the Museum of Zoölogy of the University of Michigan, not only for the helpful suggestions they have made, but also for their interest and encouragement during the progress of the study.

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* Contribution from the Department of Zoölogy, University of Michigan.

REVIEW OF LITERATURE

There are two characters which are generally used by the herpetologist in determining the sex of a turtle. The most apparent and the most widely applied character may be found in the relative length and size of the tail, which is decidedly greater in both respects in the male than in the female. Agassiz, as far back as 1857, states that the tail of the male is much larger and stronger than the tail of the female. The second criterion is found in the relative shape of the plastron. In the male the plastron is concave; in the female, it is either flat or slightly convex. Both these characters seem to be relatively constant and fairly well defined for all species of Chelonia.

Various other types of sex differences have been described in several genera and species of Chelonia. Color variations in the sexes have been recorded in only four species, and there is some question of the validity of two of these. In describing an Indian species, *Kachuga trivittata* (Dumeril & Bibron), Boulenger (1889) says: "The male *B.* (*lege K.*) *trivittata* is characterized by three black longitudinal bands on the carapace, which are absent in the female, according to Theobald, whose opinion I am inclined to endorse rather than that of Anderson, who makes a distinct species (*Batagur iravadica*) for the specimens (females and young males) without bands." The existence of a sex difference in coloration in this species cannot be considered as definitely established, for the coloration described is apparently not present in the young males, and the identity of the species is questionable. Also, Gray (1870) has stated that the three black streaks appear to be on the shell and may flake off.

Boulenger also describes a color difference in the sexes of *Emys orbicularis*, the commonest of the European turtles, as follows: "Head dark brown or black, with lighter dots, which are yellow in the female and pale brown in the male." Blake (1921) was unable to confirm this difference after an examination of the alcoholic specimens in the United States National Museum. The difference here cannot be considered as definitive, for such a slight difference in shade would require very close examination, and even individual comparison before it could be used as a sex-distinguishing character.

Davis (1887) reported a difference in the color of the eyes in the male and female box turtles, *Terrapene carolina* (Linnaeus). This character is obviously a secondary sex character, the eye of the male being red and that of the female brown.

Blake (1921), who has made the only extensive study of sex dimorphism in turtles, summarizes the sexual differences in the spotted turtle, *Clemmys guttata* (Schneider) as follows:

> Male. — Jaws always dusky; plastron always distinctly concave in the median line toward the anterior margin of femorals; mandibular stripe nearly or quite lacking (developed in one specimen); throat sparsely or rather densely speckled with yellow, the specks never (except in one specimen) aggregated forward into a blotch; tail averaging 36.8 mm. long, its preanal length averaging 12.7 mm.; supra-auricular streak little developed (except in one specimen); anterior portion of crown usually immaculate (with one or two spots on one-third of the specimens).
>
> Female. — Jaw always pale yellow; plastron never distinctly concave posteriorly along midline, somewhat depressed transversely in the region of the femorals; mandibular line always conspicuous; throat always streaked and spotted with yellow, this developed anteriorly into a blotch; tail averaging 29.6 mm. in length, its preanal length averaging 5 mm.; supra-auricular line usually well-developed; anterior portion of crown with several yellow spots.

Yerkes (1905) has suggested that the number of spots on the carapace of the male *C. guttata* is about 15 per cent less than the number present on the carapace of the female. This character, however, exhibits such great variability in number that Blake (1921) believes the slightly greater number of spots in the female to be unimportant in sex identification.

A few investigators have noted differences in the size of the male and female specimens of various species. Agassiz and Baur have both recognized that the males of *Trionyx spinifera* are smaller than the females. O. P. Hay (1891) observed a few specimens of *Graptemys-geographica* and *G. pseudogeographica*, in which the length of the carapace in the male averaged 3¾ inches and in the female varied from 6¾ to 9 inches. Hay also stated that, in these species, the head of the males is much smaller and more pointed than in the females. The smaller size of the head in the male Graptemys is to be expected, for the male is evidently a much smaller individual than the female. Whether the head is smaller in proportion to the length of the carapace or to the general size of the male than in the female, is not stated. The shape of the head, however, may constitute a sex-distinguishing character. I have had the opportunity to examine several specimens of *G. geographica,* and am able to confirm this observation with regard to carapace length.

R. E. Coker (1910), in his study of abnormalities in the horny scutes of *G. geographica,* correlated the degree of abnormality with sex. He summarizes the differences as follows: "Females show a much greater degree of diversity than males. This is true as regards both percentages of abnormal individuals and degree of abnormality in the average individual."

Agassiz (1857) describes differences in the sexes of the Kinosternidae as follows: "The difference in the form of the shield consists in the greater width of its front part in the female. The tail of the male is much larger and stronger than that of the female. There is, in the male, a patch of rough scales in the bend between the thigh and the leg."

Hallowell (1856) has observed several differences in the sexes of both young and adult individuals of *S. odoratus.* It has been impossible to check his results with my material, since the reference was not discovered until my observations were completed. I am of the opinion, however, that accurate measurements of a larger number of specimens would not confirm all the differences recorded by Hallowell.

From these cases of sex differences, it is quite evident that such characters do exist in the Chelonia. If a careful examination were made of the various species of this order, sex-identifying criteria would undoubtedly be found in every species, exclusive of the differences in tail size and plastron shape.

MATERIAL AND METHODS

During the past year and a half, I have collected, from various fresh-water lakes in the vicinity of Ann Arbor, Michigan, a series of twenty-nine specimens of the common musk turtle, *Sternotherus* *odoratus* (Latreille). This series was preserved in 10 per cent formalin after the sex had been first determined by recognized sex-characters, and verified by dissection. In addition to this material, I have examined, through the kindness of Mrs. Helen T. Gaige, a series of thirty-one individuals of this species in the Museum of Zoölogy of the University of Michigan. The total number of specimens examined was sixty, of which thirty were males and thirty females. The entire number included only animals which were obviously sexually mature.

Close observation and comparison of male and female individuals of approximately the same size and age revealed no significant sex characters, with the exception of those already known for this species. However, certain differences in the size of various exoskeletal structures appeared to be evident, and it seemed desirable to make a statistical study of those anatomical regions which might be related to sex. Measurements were made of numerous exoskeletal parts by means of a vernier caliper and recorded in millimeters; the values of the averages and their probable errors were arrived at by the use of approved statistical methods and formulae.

DATA AND DISCUSSION

Certain characters which are useful in the identification of sex in *S. odoratus* have been known for some time. The difference in the size of the tail is very marked in this species, and is probably the most valuable character for identification purposes. The general rule that the tail of the male turtle is much larger and stronger than that of the female is especially applicable to this species. The concavity of the plastron in the male *S. odoratus* is also characteristic.

Sir Richard Owen (1866) has stated that "in some Tortoises, the end of the tail has a thick epidermal sheath, which, in the male Cinosternon [Sternotherus], is armed with a pointed tip." In the key to the turtles of Michigan (Ruthven, Thompson and Gaige, 1928), the genus Sternotherus is described as follows: "Bridge short and rather wide. Tail in males with a terminal nail, and without a median dorsal row of tubercles. Marginal scutes 23." There are some exceptions to this as a sex character. I have found, in the series of thirty females examined, the terminal nail present in twelve individuals. When this nail is present in the females, it is always acutely pointed; when absent, the tail of the females is sharply pointed. In the males, the terminal nail is present in all specimens, but is rounded or blunt at the tip. A more accurate definition of this character would be as follows: *Tail in males with a blunt terminal nail.* This statement excludes those females in which the terminal nail exists. All the males examined show the absence of a median dorsal row of tubercles on the tail. Laterad to the smooth dorsal surface of the tail are two rows of six or eight tubercles, symmetrically arranged. In the females, there is a median dorsal row of tubercles on the tail; often many tubercles are arranged irregularly around the median row. They are larger and more numerous than in the males. The epidermal area surrounding the anus has also larger and more numerous tubercles in the females than in the males.

No color differences in the sexes of *S. odoratus* have been observed. The alcoholic and formaldehyde specimens are more or less unsatisfactory for the study of coloration. Consequently, although certain differences may be related to sex, I do not at this time consider the evidence as positive enough to permit an absolute statement of a sex character which is based on color differences.

In the description of this species by Ruthven, Thompson and Gaige (1928), the following statement occurs: "All of the plastral scutes in the adults separated by areas of skin." There is a distinct difference in the size of the plastral scutes of the males and the females; the scutes are smaller in the males. This difference in the size of the scutes is indicated in another manner, for the amount of flesh or skin between the scutes is greater in the male plastron (Fig. 19). Of the sixty specimens studied, one female would have been taken for a male on the basis of this character. This single specimen was also abnormal with respect to another character, and will be considered in more detail later.

As stated above, Agassiz (1857) described the sexes of the Kinosternidae as differing in the scalation of the hind legs, the males having a rough patch of scales between the thigh and the leg. This character occurs in *S. odoratus*, but it is slightly modified

(Fig. 20). In the adult male *S. odoratus*, two small round or oval patches of scales are present on each of the hind legs. Beneath the scales, the skin is hardened and very tough, resembling the foot pad of a mammal. The upper patch of scales is on the inner side of the leg and just above the knee at the distal end of the thigh. The lower patch appears also on the inner side of the leg and just below the knee at the proximal end of the crus. When the legs are drawn in, these patches lie exactly against each other. The significance of this peculiar arrangement is a matter of conjecture. It appears to be a type of grasping apparatus, and is possibly useful for support, or in grasping the shield of the female during copulation.

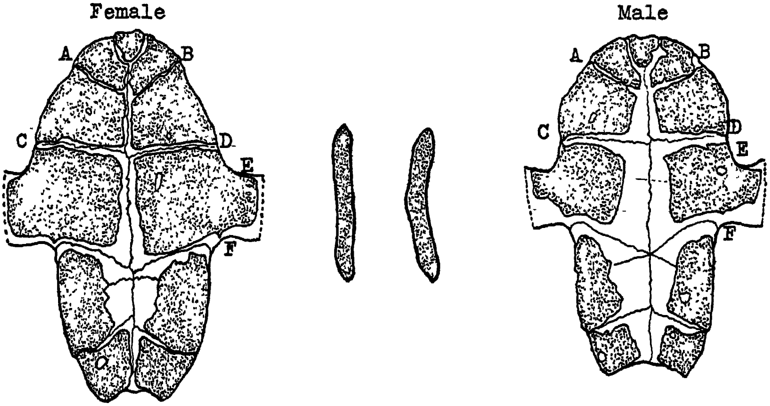

FIG. 19. Diagrams of the ventral surface of the male and female plastra; also in cross-section

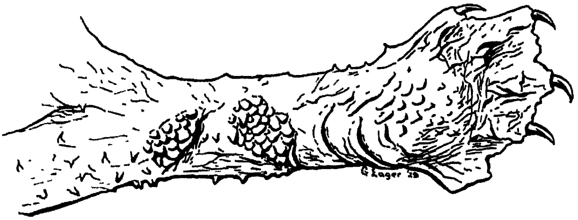

FIG. 20. Scale patches on hind leg of male *S. odoratus* (Latreille)

No difference between the sexes was expected to be found in the total carapace length. This character is often taken as an age criterion, and will be used as such in the following discussion. In the males, the length of the carapace varies from 81 mm. to 119 mm., and averages 96.02 ± 1.11 mm. In the females, the variation for this character is from 83.7 mm. to 108.9 mm., and the average value is 94.07 ± 0.75 mm. Two exceptionally large males were among the specimens measured, and their presence in the sample population studied produces the slightly larger average of the males. Since the length of the carapace is a constant character for both sexes, it will be used as a basis for comparison with the other measurements taken. In the graphs accompanying this paper, the length of the carapace is plotted on the abscissa and the character with which it is compared on the ordinate.

In order to determine how great a difference existed in the tails of the two sexes, and exactly how the difference was expressed, measurements were made of six regions of the tail, in six different ways. The differences which appear will be considered in the order of their importance in the identification of sex.

1. *Length of the tail from the anal notch to the tip, or the total length.* —The smallest male examined measured 25.8 mm., and the largest one 41.8 mm. for the total tail length. The mean value and the probable error is 33.72 ± 0.43 mm. The females examined varied in measurement of the total tail length from 17.3 mm. for the smallest specimen to 27.8 mm. for the largest. The mean value and probable error for the females is 22.31 ± 0.41 mm. As was expected, the difference between the males and females with respect to this character is very pronounced. The difference between the averages indicates that the tail of the male is nearly half again as long as that of the female. Graph A (Fig. 21) pictures the difference in relation to the length of the carapace, which is constant in the sexes and is characteristic of the age of the individuals. Expressed in percentage of the carapace length, the tails of the males average 36 per cent; those of the females, only 23 per cent of the carapace length. If a frequency curve were plotted on the basis of this percentage value, there would be no overlapping whatsoever.

2. *Length of the tail from the caudal edge of the carapace to the tip.*

— The sex of the individual is very easily determined when the animal is in motion, by observation from the dorsal side. The length of the extended tail of the males is visibly greater than in the females, when viewed dorsally. In the males, this length of the tail varies from 18.7 mm. to 27. 6 mm., and averages 24.37 ± 0.30 mm. In the females, the variation in this character extends between the limits of 7.1 mm. and 16.7 mm., and the average value

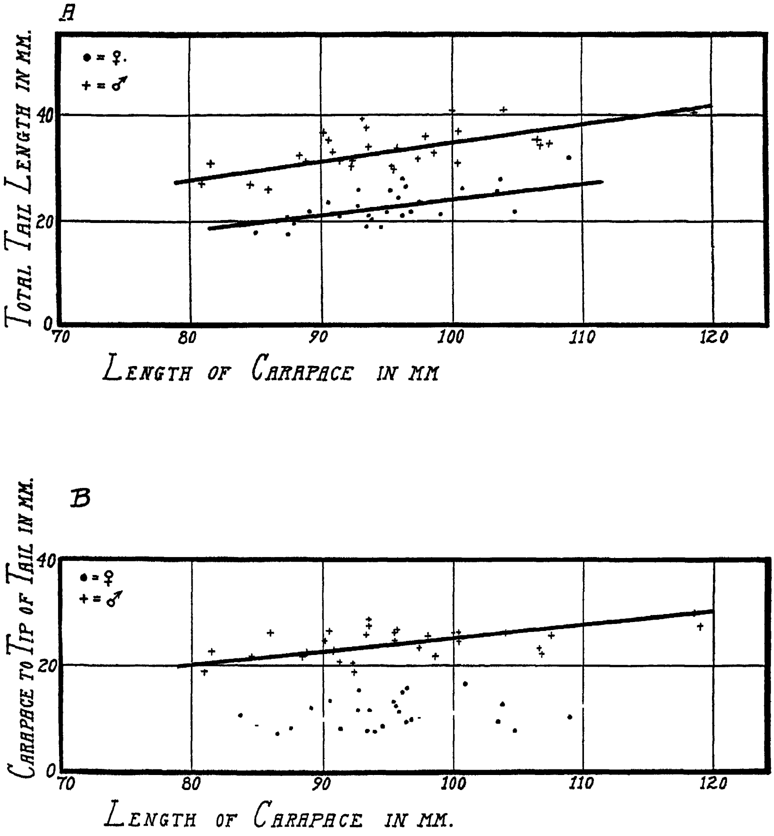

FIG. 21. Graphs showing (*A*) the length of the tail from the anal notch of the plastron to the tip, and (*B*) the length of the tail from the carapace to the tip, for both males and females, in relation to the length of the carapace

is 10.8 ± 0.32 mm. No overlapping occurs in any of the measurements, and the average value of this character in the males is more than twice that in the females. Graph B (Fig. 21) demonstrates this sex difference as being exceptionally distinct.

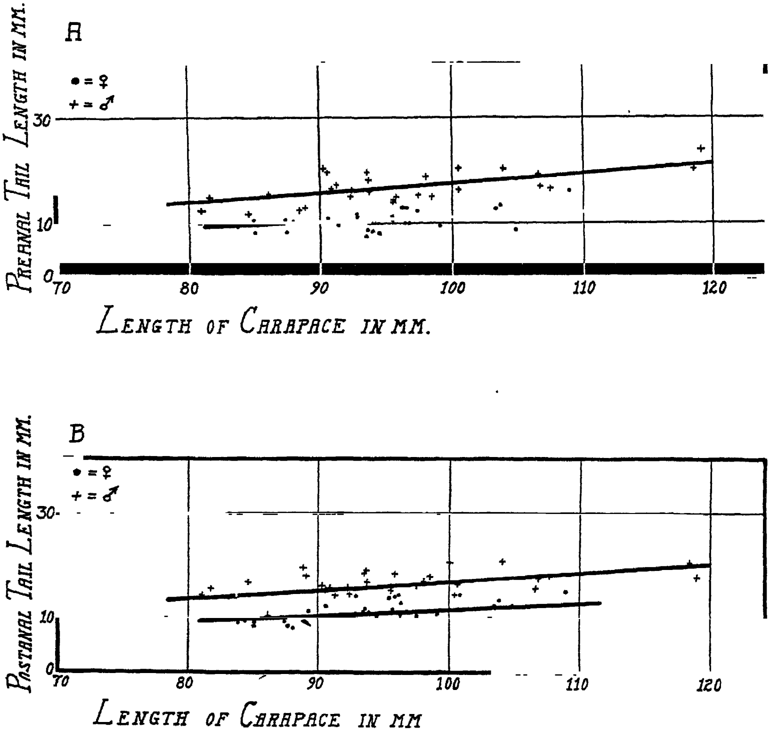

Fig. 22. Graphs showing (*A*) the preanal length of the tail, and (*B*) the postanal length of the tail, for both males and females, in relation to the length of the carapace

3. *Distance between the anal notch of the plastron and the center of the anus, or the preanal tail length.* — Graph A (Fig. 22) shows a well-defined difference between the sexes in this character. The males vary in preanal tail length from 11.9 mm. to 24.4 mm., and average 16.92 ± 0.35 mm. The females vary in this respect from 7.7 mm. to 16.7 mm., and average 10.76 ± 0.23 mm.

4. *Distance from the center of the anus to the tip of the tail, or the postanal tail length.* — This measurement was determined by taking the difference between the total length of the tail from the plastron to the tip and the preanal length, in order to eliminate as much as possible of the error involved in measurement. The postanal length of the tail in the males varies from 10.4 mm. to 20.8 mm., and averages 17.19 ± 0.27 mm. The females vary for this character from 8.7 mm. to 15.3 mm., and average 11.32 ± 0.23 mm. Graph B (Fig. 22) shows the sex difference in this character.

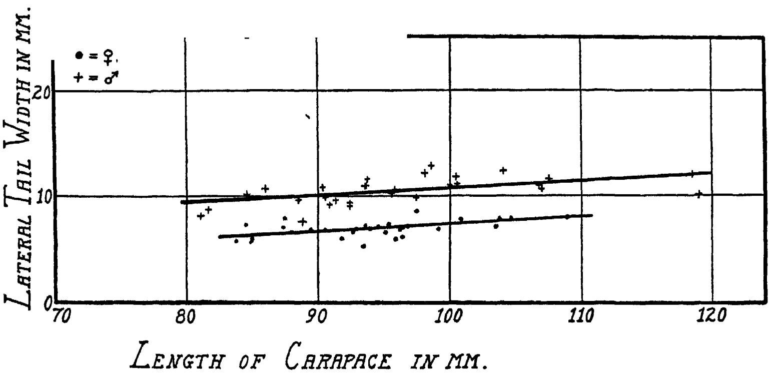

Fig. 23. Graph showing the lateral width of the tail at a point midway between the anus and the plastron, for both males and females, in relation to the length of the carapace

The figures cited by Blake (1921) do not show a difference in the postanal length of the tail in the sexes of *C. guttata.*

5. *Lateral width of the tail at a point midway between the anus and the plastron.* — Blake (1921) states that, in *C. guttata,* the tail of the female is perhaps more slender than that of the male, but that variation seems too great to make this difference of any diagnostic value. The following data (see Fig. 23) shows that in *S. odoratus* the tail of the females is compressed laterally to a marked degree. The males vary in tail width from 7.6 mm. to 13.0 mm., and average 10.39 ± 0.13 mm. In the females, this character varies from 5.7 mm. to 8.6 mm., and averages 6.86 ± 0.09 mm. The males exhibit a greater variation in this character than do the

females, probably depending upon the position of the hemi-penis in the cloaca.

6. *Dorso-ventral thickness of the tail at a point midway between the anus and the plastron.* — The sex difference in this character is not apparent when the numerical averages of the two sexes are compared. The males vary in this respect from 8.2 mm. to 15.1 mm., and average 12.3 ± 0.19 mm. The variation of this character in the females is not as wide as in the males, for the smallest measurement is 10.02 mm., and the largest 14.9 mm. for the females. The average measurement in the females is 12.65 ± 0.14 mm.

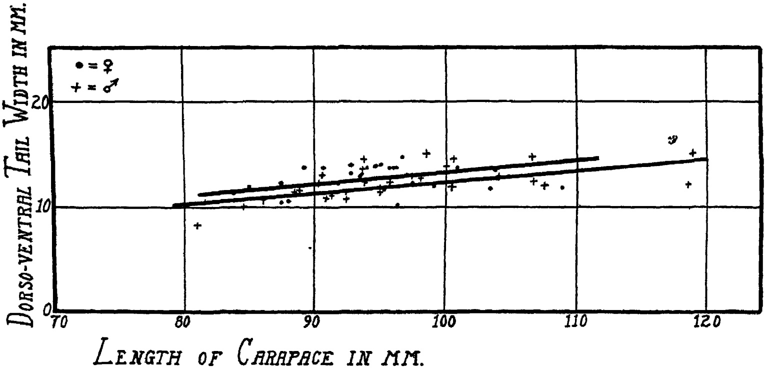

FIG. 24. Graph showing the dorso-ventral thickness of the tail at a point midway between the anus and the plastron in both males and females, in relation to the length of the carapace

When, however, this measurement is plotted against the carapace length (Fig. 24), a slight difference is apparent. Variation is too great and the difference between the sexes too small to permit one to consider this character of diagnostic value in sex-determination. It may be said that there is a tendency for the tails of the females to be wider dorso-ventrally at a point between the anus and the plastron than are the tails of the males. A comparison of the numerical means for this character with those for the lateral width of the tail demonstrates the difference in the shape of the tail of the males and females. On the basis of this comparison, the tail of the males between the anus and the plastron is nearly circular; that of the females is strongly compressed laterally.

The figures quoted above and the graphs convince one that a considerable difference exists in both size and shape of the tail in the two sexes. They also demonstrate the extent of these differences and define their anatomical position.

The preanal length of the tail as defined above, namely, that portion of the tail between the anal notch of the plastron and the center of the anus, is not a true preanal portion of the tail, but is modified by the presence of the plastron. It is quite possible that the difference found in the preanal length of the tail is due not to an actual difference, but to an extension of the plastron posteriorly in the females. If the plastron length is greater in the females than in the males, the preanal length of the tail would be proportionally shorter. Measurements were made of the length of the plastron along the median line from the anal notch to the anterior edge. Variation of the plastron length in the males occurs between 53.5 mm. and 82.2 mm. The average length of the male plastron is

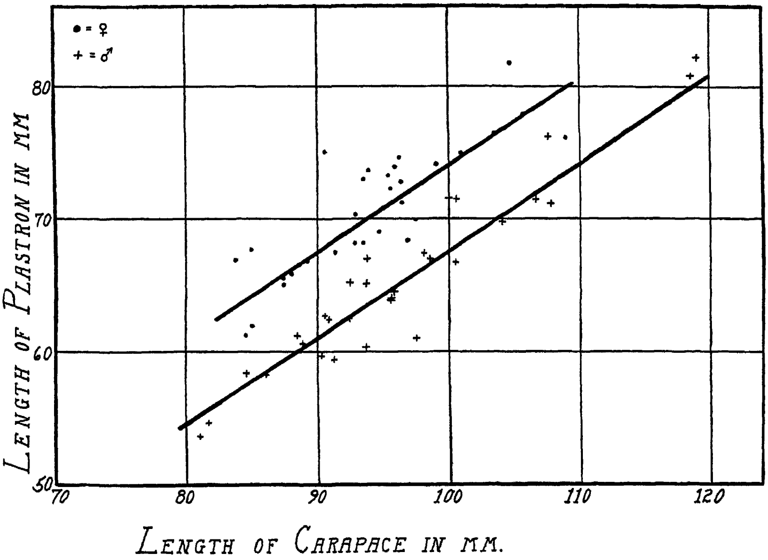

FIG. 25. Graph showing the length of the plastron for both males and females, in relation to the length of the carapace

65.34 ± 0.84 mm. The female plastron varies from 61.3 mm. to 81.9 mm. in length and averages 70.97 ± 0.52 mm. A slight difference which is not insignificant exists. This difference is not quite great enough, however, to counterbalance the difference between the sexes in the preanal length of the tail, although it lessens the difference in preanal tail length to a great extent.

The difference in plastron lengths is not significant enough to be of value as a sex criterion in itself. When compared with the carapace length (Fig. 25), a pronounced difference appears. Expressed in percentage of the carapace length, the plastron length of the males averages 67.92 per cent of the carapace length; that of the females, 75.02 per cent. Two females of the thirty specimens examined are overlapped by four of the thirty males studied. One of these females was also aberrant with respect to another character and was briefly mentioned above. Upon dissection this specimen proved to be a normal female with regard to the internal reproductive organs; no abnormalities were noted. The abnormality may be caused by a failure of the female character to be expressed because of the inactivity of the ovarian hormones during the developmental period, but this is, of course, only a conjecture.

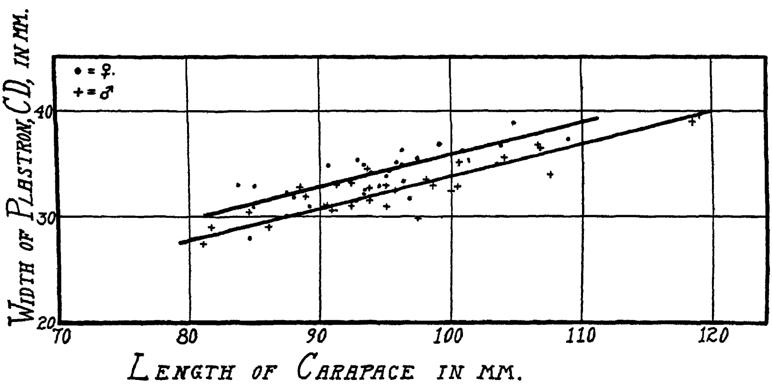

FIG. 26. Graph showing the width of the plastron across the posterior edge of the humeral scutes (Fig. 19 C D), for both males and females, in relation to the length of the carapace

A slight sex difference is manifested by measurements taken of the width of the plastron across the posterior edge of the humeral scutes (Fig. 19 C D). In the males, this character varies from 27.3 mm. to 39.6 mm., and the average is 32.72 ± 0.34 mm. In the females, the plastron at this point varies from 28.0 mm. to 38.9 mm. in width, and averages 34.96 ± 0.33 mm. This difference is valueless as a criterion for the identification of sex. That a difference does exist is more easily understood by plotting the width of the plastron at this point against the length of the carapace (Fig. 26). The curves obtained demonstrate a slight overlapping, but show that the greater portion of the females lies above the width of this character in the males.

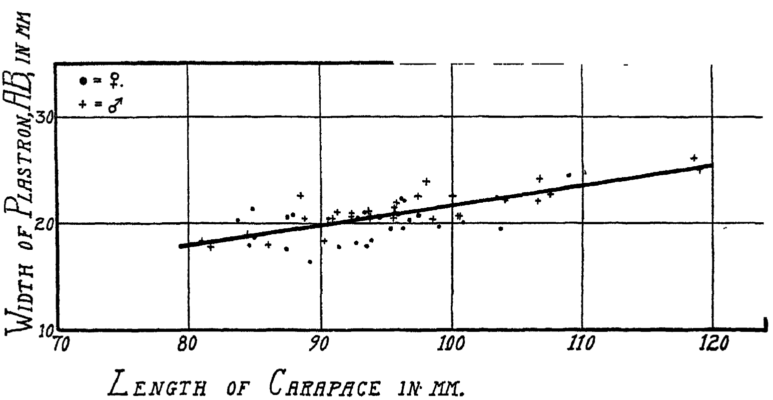

FIG. 27. Graph showing the width of the plastron across the posterior edge of the gular scutes (Fig. 19 A B), for both males and females, in relation to the length of the carapace

Measurements taken of the width of the plastron across the posterior edge of the gular shields (Fig. 19 A B) show a very small difference, which is insignificant in itself, between the males and the females. The smallest plastron width for the males is 17.7 mm. and the largest 24.8 mm. The average male plastron is 21.15 ± 0.24 mm. wide at this point. In the females, the plastron width across the gular shields varies from 16.4 mm. to 24.9 mm., and averages 20.05 ± 0.20 mm. Comparison with carapace length (Fig. 27) shows no actual difference between the sexes in this character. If a frequency curve is plotted for this character in both sexes on the basis of its percentage of the width of the plastron at the posterior edge of the humeral scutes, a bimodal curve will be obtained. This percentage in the males varies between 58.7 and 75.2 per cent, and averages 64.6 ± 0.45 per cent. In the females, the percentage varies from 51.2 to 65.4 per cent, and averages 59.4 ± 0.5 per cent. Although neither of the two latter characters can be of value in sex-identification if used separately, the use of them in relation to each other may assist in distinguishing sex. The plastron of the female is narrower at the anterior end than that of the male, with respect to the width of the plastron at the posterior edge of the humeral scutes.

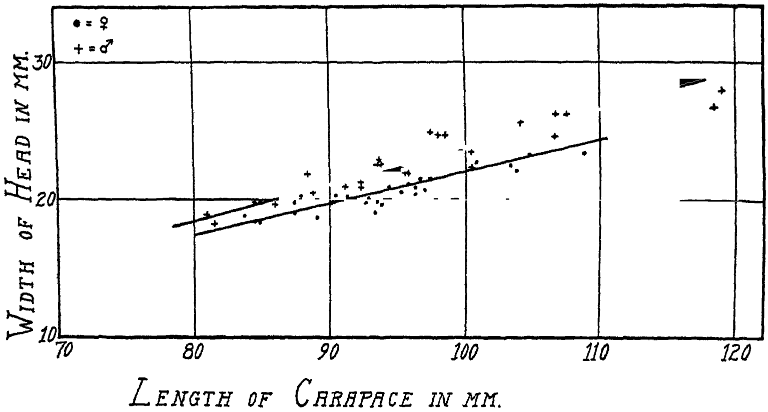

FIG. 28. Graph showing the width of the head in both males and females, in relation to the length of the carapace

The width of the head is a common character which apparently is often different in the two sexes. There is a slight correlation in *S. odoratus* between sex and head width. The measurements were taken at a point immediately anterior to the tympanic membrane, where the head reaches its maximum width. The male head width varies between 18.9 mm. and 26.8 mm., and the average head width is 22.68 ± 0.3 mm. In the females, the head width varies between 18.4 mm. and 23.4 mm., and averages 20.66 ± 0.21 mm. Figure 28 shows graphically the slight difference between the sexes in this character. The difference in head width seems to increase with the age of the individual.

A careful comparison of male and female individuals seemed to indicate that there might be a difference in the width of the bridge which connects the plastron with the carapace (Fig. 19 E F), the bridge of the females being slightly wider than that in the males. Measurements of the width of the bridge at its narrowest point have borne out the observed difference. The width of the bridge in the males varies between 18.40 mm. and 15.4 mm., the average being 11.81 ± 0.21 mm. In the females, the bridge width varies from 11.4 mm. to 23.4 mm., and averages 14.00 ± 0.20 mm. A graph (Fig. 29) which compares this character with the carapace length demonstrates its value as a sex-distinguishing character.

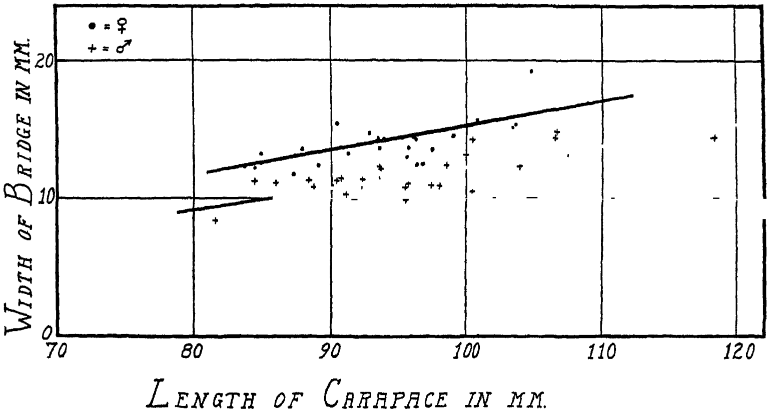

FIG. 29. Graph showing the difference in the width of the bridge of both males and females, in relation to the length of the carapace

Measurements of the width of the carapace taken on a line lying between the second and third vertebral scutes show no difference between the sexes. When considered with respect to carapace length (Fig. 30), a slight difference is noted. The males vary between 51.5 mm. and 75.4 mm., and average 63.08 ± 0.68 mm. in carapace width. The female carapace varies from 56.9 mm. to 74.1 mm. in width, and averages 63.84 ± 0.47 mm. The variation is much too great for this character to be of any use in sex diagnosis. That an actual difference exists in carapace width is not well established, possibly because of the small number of specimens.

CONCLUSIONS AND SUMMARY

The sex differences described may be divided into two groups or types, those useful in sex identification in the field or laboratory, and those which are of purely morphological interest.

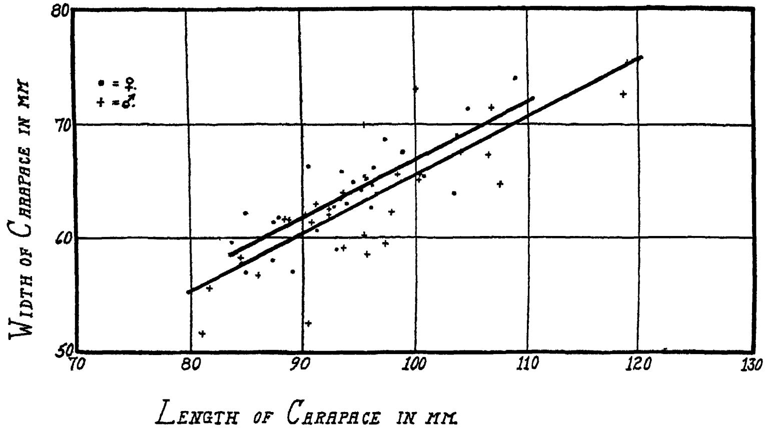

Fig. 30. Graph showing the difference in the width of the carapace of both males and females, in relation to the length of the carapace

The first group of sex characters are qualitative and may be summarized as follows:

Males. — Tail with a blunt terminal nail, and without a median dorsal row of tubercles; hind legs with two scale patches on median side of knee; plastron concave; tail round in cross-section between the anus and the plastron; plastron length below 70 per cent of carapace length.

Females. — Tail with or without terminal nail, which, if present, is acutely pointed; tail with a median dorsal row of tubercles; plastron flat or slightly convex; plastron length above 72 per cent of carapace length.

If the percentage of plastron length and carapace length lies between 70 and 72, the sex cannot be considered as definitely established on the basis of the latter character.

The following differences are quantitative, but are useful in distinguishing sex when comparisons are made of several individuals:

1. Total length of tail from plastron to tip greater in male than in female.
2. Length of tail from the carapace to the tip greater in male than in female.
3. Preanal and postanal tail lengths greater in male than in female.
4. Length of plastron greater in male than in female.
5. Width of bridge connecting the plastron and carapace greater in female than in male.
6. Width of head greater in male than in female, and more pronounced in the older males.
7. Width of plastron across the posterior edge of the humeral scutes greater in female than in male. There is no difference in the plastron width across the posterior edge of the gular shields.
8. Amount of skin on plastron between scutes greater in male than in female.
9. Plastral scutes smaller in male than in female.
10. Tubercles on the tail larger and more numerous in the female than in male.
11. A slight difference in the width of the carapace, in which the female is greater than the male, is indicated. Variation is, however, too great to allow this character to be used in sex identification.

No sex difference is found in the length of the carapace.

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BEAVER PLANTINGS IN MICHIGAN

HARRY D. RUHL AND PARISH S. LOVEJOY

DURING the summer of 1928 field officers of the State Department of Conservation were asked to show on maps the reaches of our northern streams which were plentifully stocked, fairly well stocked, suitable for beaver but unstocked, and unsuited for beaver; also locations where beaver had become a nuisance, and places where the planting of beaver would be desirable.

Although this first inventory is far from accurate, it can readily be corrected and extended from year to year.

The following table summarizes the first inventory, the estimates of which are probably conservative:

Preliminary Beaver Inventory *

Items reported	Estimated total number of miles of stream		
	Lower Peninsula	Upper Peninsula	Total
"Lots" of beaver	10	339	349
Plenty of beaver	557	2547	3104
Some, but not enough	560	1869	2429
Suitable for planting	944	321	1265
Unsuitable for beaver	911	1088	1999
Condition unknown	252	362	614
Items reported	Estimated total number of places		
	Lower Peninsula	Upper Peninsula	Total
Necessary to trap	4	54	58
Suitable for planting	264	95	359

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* Except Lake and Newaygo, counties below town line 20 were not considered.

Beginning about August 1 and continuing into November of 1928, shipments of beaver which were live-trapped in places where they were doing damage, were made to six different state game refuges in the Lower Peninsula where there were no beaver, where reasonable protection could be expected, and where they could be kept under observation.

These shipments could not be anticipated in advance and complete details of age, sex and colony or family relationships are not available. Sometimes a shipment contained two or three beaver from the same place, but more often only one beaver was received from a locality. Shipments continued over a period of several weeks and usually all the beaver arriving at a refuge were liberated at the same place on the refuge.

Six beaver were received at the Crawford Refuge, near Grayling, and planted at the outlet of Portage Lake, a sand bottom lake with gradual slope and shores supplying considerable poplar, white birch and soft maple. They apparently left the lake after some exploration, and gradually moved down Portage Creek through five or six miles of cedar swamp with some scattered poplar available, and then through five or six miles of more open country with considerable poplar close to the stream. This stream has numerous holes five or six feet deep and appeared to be satisfactory beaver country. These beaver are now reported to be utilizing the banks and deep holes of the Manistee River and cuttings are reported on the Manistee from three miles above Portage Creek to as much as ten miles below it.

Six beaver were liberated on a small stream within the Tawas Refuge, near the National Forest Headquarters. Two beaver are living in the swimming hole of a private citizen about three or four miles below where they were planted, and have constructed a burrow in the bank and a dam against a low log foot-bridge. They are now very tame and do not stop working when under observation. Other beaver work is reported several miles farther down the stream.

Two adults and three young beaver were planted on Elliot Creek, a small stream within the Iosco Refuge. One of the adults, which was later found dead, seemed to have been caught by falling timber, but the evidence was not conclusive. These beaver ranged through suitable country along some five miles of this stream during the first two weeks or so, and then started a dam about October 24. At the same time they were working on a house about forty rods above the dam, and about January 6 they started a second dam twenty rods below the house. This creek has abundant poplar and is open all winter. During the winter they did some plastering to their house or added a little to their dam, but they did no logging in the snow.

Nine beaver were liberated on one of two small bog lakes, known as the Cutting and Damon lakes, which are about one quarter of a mile apart and within the Ogemaw Refuge. A lodge was constructed on each lake and considerable fall cutting was done. Two beaver were seen on the larger lake on several occasions, and there are, presumably, a pair to each lodge.

A dam about two hundred feet long and with water about three or four feet deep above it has been constructed across a small creek about one quarter of a mile north and a little east of the original planting. A large lodge and a small one have been constructed in the pond made by this dam.

One or more beaver apparently explored the entire vicinity, for cuttings were seen on Grass Lake about three miles from the original planting. A beaver was reported as seen on Clear Lake, and cuttings were reported on Town Line Lake. Grass, Clear, Mud, Piper, and Town Line form a string of lakes about a quarter to a half mile apart, but they are not directly connected with Cutting and Damon lakes by water.

Two adult beaver, thought to be of opposite sex and known to be from different colonies, were marked, placed in a pen together for a week, and then released on October 30 in the lake in front of the keeper's house on the Gladwin Refuge. These beaver apparently began work within a short time and stored a great deal of poplar. They did not build a lodge since this lake has a firm bottom and good banks. So far as known, they did not leave the immediate vicinity of the lake, except to explore the neighboring beaver pen at the spring inlet to the lake.

An adult female and two yearlings from the same colony and a kit from a different colony were marked, placed together in a pen for a day, and released on October 24 in Little Trout Lake on the Gladwin Refuge. They explored the inlet and springs around the lake for several days and then began to construct a lodge on the bank and to store poplar under an old dock. One or more beaver apparently were using enlarged muskrat burrows at the outlet of this lake, and living more or less independently from the other group. No cuttings were found down the outlet for several weeks, but the keeper has recently reported that only one beaver is now left in the lake, and that several beaver are using an old dam about three miles down the outlet.

Ten beaver were liberated on the Midland Refuge near Sanford. They are reported to have constructed two dams and a house on one small unnamed stream, two dams on Black Creek and a dam and house on an old county ditch. Cuttings are reported from some ten or twelve sections of land in the vicinity.

In addition to these plantings, a number of isolated colonies, some of which have escaped from beaver farms, furnish opportunity for study. These new colonies are located as follows: About one-half mile from Scotts in Kalamazoo County; near Howell in Livingston County; south of Rogersville in Genesee County; a few miles northeast of Morley in Mecosta County; on Hungerford Lake in Newaygo County; near the head of the north branch of the White River in Oceana County; on the north branch of the Pentwater River near the boundary line between Mason and Oceana counties; and on Wolf Creek within the Higgins Lake State Forest in Roscommon County.

CONCLUSIONS

1. According to present information, there seems to be no difficulty in getting beaver to settle and winter even if planted as late as November 1 and under conditions similar to those of 1928. Further check-up on the spread, mating and increase will be necessary in order to establish the actual success of these plantings.

2. Though it seems easy to pick out a number of places where beaver will probably settle, there is no assurance that they will remain in any particular locality.

3. Where large streams are available, we expect new plantings to "bank it" rather than build dams and lodges as on the smaller tributary streams.

4. We have no definite information whether these beaver have grouped in mated pairs or whether individuals of the same sex may be found living together.

5. The reasons for consolidation or split-up are not clear.

6. Whether there will be additional shifting during the spring or summer remains to be determined.

7. Whether satisfactory pairing can be secured from unselected animals planted in small numbers is uncertain; the number necessary for efficient colonization has not been determined.

8. Since the original number of planted animals is known, there is opportunity to determine the amount of cutting, food used and work done per beaver over a winter period.

9. These plantings, together with several isolated colonies many of which have escaped from beaver farms, offer special opportunity to study the spread, increase and influence of beaver on other wild life, under various stream and cover conditions.

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OBSERVATIONS ON THE SEASONAL ACTIVITIES OF THE WHITE-TAILED PRAIRIE-DOG, *CYNOMYS LEUCURUS* *

ALFRED H. STOCKARD

I. INTRODUCTORY

PRAIRIE-DOGS are quite generally distributed over the western part of the United States, occupying the territory lying between Canada and Mexico on the north and south and between central Kansas and central Utah on the east and west. They are usually regarded by agriculturists as pests and have been the objects of numerous eradication campaigns which have practically exterminated them from the more intensely grazed and cultivated localities in their range. With the gradual decrease of their natural enemies, such as badgers, coyotes, foxes and ferrets, prairie-dogs find man and food-supply the chief factors limiting their increase. (See Merriam, 1901.)

Prairie-dogs live in burrows grouped in colonies or "dog-towns" which may vary in size from a dozen to several thousand burrows; there may be as many as one hundred and fifty burrows to the acre. The "towns" seem to be located with reference to drainage, nature of subsoil and food-supply. The animals appear to prefer sloping or rolling ground to a flat or sharply hilly terrain, and clay subsoil to rock, gravel or sand. Towns are usually found not on areas barren of vegetation or under cultivation, but on grassy areas devoid of larger vegetation, except possibly scattered mesquite trees or sage bushes. They seem to be located without reference to water, and apparently the animals never drink in the wild state.

The genus *Cynomys* belongs to the family Sciuridae and is divided into two subgenera and seven species and subspecies. The most conspicuous constant character separating the two subgenera is the color of the tip of the tail; two of the species have black-tipped tails and three, white-tipped tails. The black-tail group inhabits the plains and the white-tail group the mountain valleys. The range of each form is sharply defined, since there are only a few localities in which overlapping of ranges is known to occur. *C. leucurus*, the type species of the white-tail group, ranges over central and southern Wyoming, northeastern Utah and northern Colorado, inhabiting the mountain valleys at an altitude of 5000 to 8000 feet (Hollister, 1916; Cory, 1917).

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* Contribution from the Zoölogical Laboratory of the University of Michigan.

In view of the range of the genus, the density of the population, the size of the animals, their conspicuousness and the ease with which they may be secured, it is indeed surprising that so little scientific study has been made of these interesting animals. They have been known to zoölogists since the Lewis and Clark Expedition of 1804. Aside from limited observations regarding taxonomy, distribution, natural history and control measures, in spite of their many distinctive traits, there is very little mention of prairie-dogs in literature.

II. GENERAL ACTIVITIES

The daily and seasonal activities of the white-tailed prairie-dogs are in many ways very interesting. If feeding is used as a criterion for measuring activity, they appear to be diurnal. Analyses of stomach contents indicate that they feed only during daylight, and that the principal feeding hours are in the afternoon. Table II shows the average gross weight of the stomachs of nineteen adults taken between the hours of 10:00 A.M. and noon to be thirty-two grams; that of seventy-three adults taken during the same season, but between the hours of noon and 6:00 P.M., is ninety-one grams. Also, they are to be seen out of their burrows in greater numbers on bright days and near mid-day than on cloudy days or in the late afternoons. Animals kept in the laboratory have been observed, however, to feed both day and night.

Likewise, the annual season of activity seems to be limited to a short period. The animals begin to appear in numbers on the warmer days about March 1 and live a very active life until mid-July. Though the young remain active after this date, the adults quite suddenly disappear and very few are seen again until the following spring. By autumn the young have grown to almost mature size and cannot easily be distinguished from the adults. To judge from their behavior under laboratory conditions, it seems possible that the adults may reappear for a period of activity in the autumn, but attempts at collecting during this season give results which do not support this possibility. By November 1 prairie-dogs are very rarely seen, though they have been reported out on warm days during all the winter months (Merriam, 1901).

III. REPRODUCTIVE ACTIVITIES

My collections indicate (see Table I) that the males appear before the females in the spring early in March. The exact time varies with the advancement of the season and the altitude and exposure of the locality. They are followed about two weeks later by the females. On first appearance they are in good condition and have a reserve of fat stored beneath the skin and around the viscera. At that time the males seem to be sexually functional. The testes and accessory glands are very much enlarged and distended. Soon after the appearance of the females copulation occurs, and continues within a time limit of two or three weeks for the entire population in a given locality (see Table I). After this period a rapid decrease in size and content of the sex glands of the males occurs until they are approximately only one tenth of their previous weight. Collections throughout the summer indicate that there is only one breeding season during the year.

After a gestation period of twenty-eight to thirty-two days, from two to ten young, usually five or six, are produced in each litter (Table III), born approximately between April 20 and May 8 (Table I). The young at birth are quite helpless, blind, hairless, and with undeveloped auditory meati and pinnae. They develop slowly, becoming covered with hair at about ten days of age and opening their eyes during the fifth week. They probably come above ground before they are six weeks old, but may not gather enough food to live without milk from the mother before the end

TABLE I

Times of Appearance, Breeding and Parturition in the White-tailed Prairie-dog, *Cynomys leucurus*

Date	Number of animals taken	Number of males	Number of females	Number pregnant or recently with young	Number recently with young
Record for 1927					
3–8	2	2	0	0	0
3–14	4	4	0	0	0
3–24	1	1	0	0	0
3–27	3	2	1	0	0
3–30	5	1	4	0	0
4–2	11	11	0	0	0
4–5	12	2	10	9	0
4–9	12	7	5	4	0
4–19	2	2	0	0	0
4–23	3	0	3	2	0
4–25	5	1	4	3	0
4–30	8	6	2	2	0
5–7	24	12	12	8	8
Record for 1928 *					
3–20	1	1	0	0	0
3–21	3	3	0	0	0
3–23	1	1	0	0	0
3–24	2	2	0	0	0
3–27	2	1	1	0	0
3–31	4	4	0	0	0
4–1	10	5	5	5	0
4–2	1	0	1	1	0
4–4	12	0	12	12	0
4–10	11	3	8	8	0
4–14	16	5	11	10	0
4–17	12	4	8	8	0
4–20	7	3	4	3	0
4–22	9	0	9	8	1
4–27	10	3	7	7	2
5–1	9	3	6	5	3
5–8	12	3	9	9	9
5–12	9	3	6	3	3
5–19	7	4	3	3	3

* This table does not include all males taken during 1928, since only representatives of each lot taken were desired for study of the sexual cycle in the males.

TABLE II

HOURLY AND SEASONAL VARIATIONS IN STOMACH CONTENT IN THE WHITE-TAILED PRAIRIE-DOG, *Cynomys leucurus*

Date 1927	Number taken in forenoon	Number taken in afternoon	Average body weight in grams	Average stomach weight in grams
Before breeding season				
3–8	0	2	963	88
3–14	4	0	868	26
3–24	0	1	850	74
3–27	3	0	798	30
3–30	5	0	643	29
During breeding season				
4–2	0	11	773	44
4–5	0	12	677	79
4–9	0	12	763	74
After breeding season				
4–19	0	2	755	92
4–23	0	3	857	130
4–25	0	5	721	94
4–30	0	8	904	123
5–7	7	0	861	40
5–7	0	17	927	128
Average for	19 =		795	32
Average for		73 =	811	91

TABLE III

NUMBER AND DISTRIBUTION OF EMBRYOS IN 67 PREGNANT UTERI OF *Cynomys leucurus*

	Number of embryos in each group recorded											Total	Average
	0	1	2	3	4	5	6	7	8	9	10		
Number of groups in right horns......	0	8	18	15	23	3	0	0	0	0	0	196	2.93
Number of groups in left horns........	5	8	18	22	11	1	2	0	0	0	0	171	2.55
Number of groups in complete uteri....	0	0	2	0	11	21	20	12	0	0	1	367	5.48

of the seventh week. They soon become voracious eaters, and grow more rapidly, reaching almost full size by the end of the autumn (Johnson, 1927). It is doubtful whether they reach sexual maturity, however, until they are two years of age, since occasionally immature animals of both sexes are taken in early spring.

IV. FEEDING ACTIVITIES

The food of prairie-dogs is principally vegetation. An examination of the stomach contents of ninety-two taken during the spring of 1927 revealed weed and grass seeds, cactus roots and stems, moss, sage leaves, grass and insects. The early collections were made before the snow was completely gone; some of the animals had dug out through several inches of snow which had drifted into the burrows. Dry vegetation and cactus roots predominate as food at this time, but the animals turn to green food as soon as it appears.

The number of insects found in stomachs was variable, ranging from none in most stomachs to approximately one hundred beetles in one. Insects persisted in the diet throughout the spring period, being for the most part the common inhabitants of the burrows. In view of the eradication campaigns being conducted, a thorough study of the insectivorous habits of this animal should be made.

An interesting relation between breeding activities and voracity occurs. Comparisons indicate that the males eat voraciously before the appearance of the females, that the entire population eats less during the breeding period, and that after this period voracity reaches its peak (Table II). The stomach of an animal in late spring may constitute more than one sixth of its body weight. The period of highest voracity coincides with that of greatest abundance of succulent vegetation. A rainy period usually extends over the latter part of April, May and early June (Bigelow, 1908). During this time vegetation is abundant, but it soon becomes parched in the dry summer months which follow. During July the adults withdraw into their burrows, and necessarily the rate of feeding decreases.

As is to be expected from the short duration of the foraging season, the weight changes of the animal are great during the year.

Adults taken at the close of the hibernation period vary in weight between six hundred and one thousand grams. By June 1 the weight range has increased to from eight hundred to thirteen hundred grams; this increase is due mainly to an enormous amount of fat stored for the long period of relative inactivity from midsummer until early spring.

V. HABITATIONS

The burrows of prairie-dogs are very long and often extend deep into the ground. A burrow of *C. ludovicianus* was dug out by W. H. Osgood (Merriam, 1901) and reported to be approximately thirty-five feet long and fifteen feet deep. At this depth the animals are able to pass the winters under more or less uniform temperature conditions. The burrows serve as harbors for numerous insects, many of which probably pass the winter there, as is indicated by their escape in great numbers in early spring. Among these insects one of the most interesting is *Viatica spinosa* Garrett,[1] a dung-fly of the family *Helomyzidae*. In early spring as many as two hundred are often found perched on the roots of the hairs on the tail of prairie-dogs. They are present on most specimens taken early in the season, but in decreasing numbers after mid-April and rarely after May 1. On warm days in the latter part of April, they are often seen in enormous numbers crawling out of the mouths of the burrows. Apparently they spend the winter attached to the tails of the prairie-dogs or resting otherwise in the burrows.

VI. HIBERNATION

The condition in which prairie-dogs pass the winter in nature is not known with certainty. Two specimens kept in the laboratory during the past year (1928–29) became relatively inactive at ordinary room temperature about mid-summer and went into hibernation early in October, remaining so with some interruption due to disturbances from handling or high room temperatures until February 1, at which time they began to eat food that had been before them for four months untouched, and passing droppings, which had not occurred for four months. Another animal, confined without food and water from June 1 to November 20, 1927, was in profound sleep from some time before August 1 to the end of the period except for short intervals when disturbed by handling. This sleep was possibly a response to extreme conditions, however, and not a normal summer behavior.

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[1] This fly has been known since 1908, when a single specimen, discovered in the Yosemite Valley by C. B. D. Garrett, was described by him and classified as *Viatica*, a new genus (Garrett, 1924). Specimens taken from prairie-dogs were identified by Mr. J. M. Aldrich, associate curator of the U. S National Museum.

While in profound sleep the animal is habitually curled up, with its nose against the lower abdomen, its tail curled under, its front feet along the sides and hind feet extended upward. It sits in this position on the broad lumbo-sacral region which is padded with subcutaneous fat. The eyes and mouth are closed, the respiratory movements are not visible, the heart beats cannot be detected by palpation, and the temperature is down to within one degree of room temperature. Carbon-dioxide output, as determined by respiration chamber tests conducted on the animal observed in the laboratory in the summer of 1927, averages less than one eighth that of the normal resting and sleeping condition.

VII. SUMMARY

The annual cycle of activity in the prairie-dogs of the vicinity of Laramie, Wyoming, may be summarized as follows:

1. Breaking of hibernation and emergence in March.
2. Heavy feeding of males before breeding.
3. Breeding and light feeding period in early April.
4. Voracious eating and fattening period from mid-April to mid-July.
5. Birth of young in early May.
6. Appearance of young above ground in late June.
7. Foraging of young for themselves from late June to November.
8. Withdrawal of adults to quiet from mid-July to November.
9. Hibernation of entire population from October or November to March.
10. Sexual maturing of young in the second spring.

I wish to thank Dr. Lenore Ward of the Department of Zoölogy of the University of Wyoming for assistance in collecting material and data, and Professor Peter Okkelberg, of the University of Michigan, for his critical reading and suggestions regarding this paper.

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INBREEDING AND THE FIXATION OF GENETIC FACTORS UNDERLYING THE TRANSPLANTABILITY OF CANCEROUS TISSUE *

LEONELL C. STRONG AND ARTHUR M. CLOUDMAN

IN THE establishment of the genetic theory for the transplantation of neoplastic tissue, Strong (2) has emphasized the importance of inbred strains of experimental animals. This procedure has been criticized by various pathologists interested in cancer research, who maintain that the process of inbreeding may introduce complicating factors and that, therefore, more confusion is thrown into the problem. They point out the fact that many conflicting phenomena have been encountered in their own experiments, so that, in order to clear up the situation, one must pay stricter attention to numbers and technique.

It is a well-established fact that tumors arising in individuals of stocks of "market mice" show a variable result when inoculated into a series of mice. This variation may be anywhere from zero per cent up to one hundred per cent, and it may even vary from one tissue transplant generation to the next. On the other hand, Strong has already determined that by the use of inbred stocks absolute results of transplantation are obtained. This can be predicted from genetic principles after a single experiment has been performed.

Owing to the conflicting situation that has arisen through the use of radically different procedures, it may be of value to consider the results obtained in this experiment.

Ten years ago Strong obtained a stock of albino mice from Dr. Bagg of the Memorial Hospital, New York City. The individuals

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* Presented by the Laboratory of Mammal Genetics, University of Michigan.

of this stock had been produced for at least seven years by pen matings. By this method is meant the retention of one male and many females from a certain number of young, with all other individuals discarded. This method, though not so accurate as others now used by geneticists, leads to the production of a relatively inbred stock of mice. No pedigrees or individual markings had been kept, so that one cannot maintain more than that a certain degree of inbreeding existed. Since the introduction of this stock into Strong's laboratory, careful records of all individuals produced have been kept, and pedigrees are determined with great accuracy.

During the early stages of the production of this inbred stock, many of the neoplastic growths encountered in old breeding females were used for transplants; none ever grew.

Recently, nine spontaneous albino tumors were inoculated into both albino relatives and F_1 hybrids. The use of the hybrids was necessary because of the shortage of inbred individuals since the transfer of the stock from Boston to Ann Arbor. These hybrids were produced by crossing albino females with dilute brown males obtained from the inbred dilute brown stock, a derivative of Dr. Little's inbred strain started in 1909 at Bussey Institution. The results obtained may be seen in the accompanying table.

The numbers are very small, but enough data have been obtained to indicate a very significant finding. All individuals inoculated have grown the tumors progressively, whereas, several years ago, no individual of this stock ever grew any transplantable tumor from other individuals of the same stock. With this change of "tissue specificity," there was obtained no intermediate point. All the individuals either grew all tumors progressively or they refused to grow all tumors. It is, therefore, obvious that the process of inbreeding clarifies the problems of "tissue specificity," tumor susceptibility and related phenomena.

CONCLUSIONS

1. The process of inbreeding is a means to clarify certain phenomena associated with the problem of tumor-tissue transplantation.
2. The inheritance of susceptibility to tumors arising in the

albino strain probably follows the same laws of inheritance as were determined by Little and Tyzzer (1), and later by Strong (3), to apply to other tumors arising in individuals of other carefully controlled stocks, namely, dominance.

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TABLE I

RESULTS OBTAINED BY INOCULATING NINE DIFFERENT ALBINO TUMORS INTO OTHER ALBINOS AND F_1 HYBRIDS

Name of tumor		Albino		F_1 hybrid	
		+	−	+	−
I	14905 ar	6	0	4	0
II	14905 a	20	0	19	0
III	14059 a	13	0	9	0
IV	13738 a	2	0	10	0
V	13738 b	2	0	10	0
VI	13738 c	5	0	9	0
VII	17495 a	5	0	9	0
VIII	16189 a	2	0	12	0
IX	15091 a	2	0	12	0

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BREEDING HABITS AND YOUNG OF THE RED-BACKED MOUSE, EVOTOMYS

ARTHUR SVIHLA

THERE is very little known concerning the breeding habits of the red-backed mouse, *Evotomys gapperi gapperi.* Kennicott (2) appears to have been the first one to publish on the habits of these mice. In the agricultural section of the Patent Office Report for 1857, he records that he found eight young in a nest and within several rods of this a family of five or six, which he concluded to be an earlier litter of the same parent.

The statements of Merriam (4) have been the basis for most of the information published subsequently about the home life of this rodent. He mentions collecting females containing four young each as early as the third of April and as late as the fourth of October. He says further: "I have also taken a female early in June that was nursing her second brood. Hence, it is clear that several litters are produced in a season."

The present paper deals with the breeding habits and young of *Evotomys gapperi gapperi* as observed in captivity from September, 1927, to June, 1928. The animals used were collected near Calumet, Keweenaw County, Michigan, by Dr. L. R. Dice during the summer of 1927. For the opportunity of studying the breeding habits of this mouse I wish to acknowledge my indebtedness to the Museum of Zoölogy of the University of Michigan.

In the laboratory, the mice were kept in wire cages measuring 10 × 15 × 7½ inches, the tops of which were made of wood and easily removable for handling the animals. A separate enamel pan made up the bottom of the cage and into this the wire portion fitted snugly. An aluminum pan filled with cotton served as a nesting place. The mice were fed a balanced ration of grains and meat scraps which was kept before them at all times. Water was furnished by means of an inverted test tube, the mouth of which had been constricted. Twice a week, green vegetables, such as lettuce or carrots, were fed.

In captivity, the period of gestation has been found to be seventeen to nineteen days, with seventeen days as the more usual period. These data are based on six checked matings of five different females. In each mating the male and female were placed in the same cage in the evening and separated the next morning. The length of gestation is calculated from the date of separation to the date of the birth of the litter.

The data follow:

Female	Date of separation	Birth of young	Days of gestation	Number in litter
1	April 23	May 12	19	4
2	Dec. 20	Jan. 7	18	5
6	April 19	May 6	17	4
6	May 7	May 24	17	5
10	April 22	May 9	17	5
11	May 13	June 1	19	2

Female No. 1 had previously had a litter of five young during the latter part of September, before I undertook this study.

Only one female had two litters in succession; copulation took place within twelve hours after the first litter was born. Hence, one female may have more than one litter a year. The other females were also placed with males after the birth of a litter, but impregnation did not occur. The majority of litters were born in May, but one appeared in January, one in June and one in September. The number of young in a litter varied from two to five with an average of 4.16. These data are not complete for the entire year since observations were not taken during the summer months of 1928.

The young mice are born in a very undeveloped condition. They weigh from 1.7 to 2.3 grams, averaging about 1.9 grams, at birth. They are completely hairless, except for the vibrissae which are already well developed. When first born they are pink, but within twenty-four hours the dorsal surface becomes darkly pigmented while the ventral surface still remains pink. When they are four days old, minute hairs first become visible on the back, and in seven days the characteristic red coloring of the back appears. This is contrary to the observations of Stone and Cram (6), who say that the young red-backed mice lack the rusty red tints of the adults. The mammae in this mouse number eight, pectoral 2–2, inguinal 2–2, and can easily be seen when the hair is still short and sparse on the ventral surface of the young female mouse. This character easily distinguishes the young females from the males.

In one litter the eyes of the young opened in eleven days but in all the other litters the eyes did not open until the mice were fifteen days old. As soon as the eyes open, the mice begin to run about and eat solid foods, although they are not yet completely weaned. In the one instance when the second litter appeared seventeen days after the first, the young of the first litter were weaned abruptly at that time, since the mother would have nothing further to do with them. When there is no second litter, the young have been observed to suckle for at least three weeks, although they also eat solid foods during the latter days of this period.

A female with a newly born litter of mice is very nervous when disturbed. Under such circumstances several abandoned their young and others even ate them.

Females Nos. 6 and 10 and male No. 19 were 120 days old when their first litters were born. Thus, it is apparent that the mice in this genus may breed when four months old.

Mating depends entirely upon the female, which, if she does not desire to mate, fights the male with teeth and claws, at the same time emitting sharp "chrrr's." If, however, mating is desired, the female makes only a slight effort to elude the pursuing male, taking a few steps and then halting. Copulation then takes place, after which both animals lick themselves thoroughly. Several matings may take place in as short a time as five minutes, as copulation is only a matter of a few seconds. After several copulations the female has no more desire to mate and fights the male if he is too insistent.

Before their eyes are open, the young cling tenaciously to the nipples of the mother. Even when she is suddenly disturbed and jumps from her nest, they still cling to her nipples and are dragged to a place of safety. They are not injured, although they are often dragged over rough surfaces. They assist their mother's movements by pushing against the ground with their hind legs. Should a young lose its hold during this method of transportation, it lies quietly for a little while, but soon makes its presence known by loud and persistent squeaks. The mother then usually returns and picks it up in her mouth. By taking hold of the skin of one shoulder she manages to place it belly side up between her teeth. The young then curls its forelegs and hind legs around the face of the mother. I have also seen a parent take hold of a heavily furred quarter-grown young by the nape of the neck and carry it in the same manner as a cat would carry her kitten, or a dog her puppy. Being carried belly side up sometimes seems to be unpleasant for the young mouse, since it makes little whimpering, squeaking noises.

On one occasion a mother had a rather difficult time when her five half-grown young refused to stay in the nest. The young were large, heavy and rather active and she was kept busy carrying them back one by one, seizing them wherever she could. Once she took one of them by the skin over the rump and dragged it head downward to the nest. The young, however, were too much for her, for as soon as she had taken one back to the nest and hurried off for another, the first would crawl out of the nest again. After this had happened several times, she appeared to be very excited, as shown by her rough manner of handling them. Only after the young became too tired to crawl out of the nest again did she finally succeed in keeping them together.

It may be interesting to compare the breeding data of *Evotomys* with those determined for another microtine, the eastern meadow mouse (*Microtus pennsylvanicus pennsylvanicus*). Bailey (1) says that the period of gestation is approximately twenty-one days. *Evotomys gapperi gapperi*, on the other hand, has a period of gestation typically seventeen days long, four days less than that known for *Microtus*. If we compare the weight at birth with the average adult weights of these two forms, we find that the ratios are the same for both. For example, the birth weight of *Evotomys* averaged 1.9 grams, whereas the average adult weight of seven specimens was twenty-eight grams. Thus the young weighed practically one fifteenth as much as the adult. In *Microtus* we find the same ratio. At birth the *Microtus* weighed three grams while an average of ten adults weighed forty-five grams, which is fifteen times the birth weight. It is interesting to note that the heavier form, *Microtus*, gave birth to the heavier young. The hair appeared in *Evotomys* in four days, slightly earlier than in *Microtus*, in which it appears in five days, but the eyes and ears did not open until the fifteenth day in *Evotomys*, though in young *Microtus* they opened in but eight days. Bailey says that the young *Microtus* are weaned in eleven days. I find that the young *Evotomys* still had their eyes closed at this age. There seems to be a correlation between the length of prenatal development and that of postnatal development in these forms. In *Evotomys* the comparatively short prenatal development is followed by a correspondingly longer postnatal development, whereas in *Microtus* the opposite is true.

There is a prevalent tendency to assume by analogy that the breeding habits of one animal are similar to the habits of a closely related form. For instance, the period of gestation of the muskrat has been assumed to be similar to that of *Microtus* on the ground that the muskrat is similar in structure to the meadow mouse. Lantz (3) says that in their breeding habits muskrats are not unlike field mice; the period of gestation is probably no onger than twenty-one days, as with the field mouse. One might likewise reason by analogy that the breeding habits of *Evotomys* must be the same as those of *Microtus* because the former is, as Seton (5) describes it, nothing but a "meadow mouse that has taken to the woods," just as the muskrat appears to be nothing but a semiaquatic meadow mouse. Since it has been demonstrated above that *Evotomys* and *Microtus* have entirely different breeding habits in captivity and since *Evotomys* is, perhaps, no more distantly related to *Microtus* than is the muskrat genus *Ondatra*, the fallacy of such analogy is obvious.

SUMMARY

Red-backed mice of the genus *Evotomys* were found to breed in captivity. The period of gestation varies from seventeen to nineteen days, with seventeen days as the more usual and perhaps normal period. The young are blind and hairless at birth, weighing on the average but 1.9 grams. Hair appears in four days. The eyes open in fifteen days (in one instance in eleven days). The young may be weaned in seventeen days if another litter follows the first immediately; otherwise, nursing may continue for at least three weeks. Both males and females are sexually mature at about four months of age; the females bear young at that time. At least two litters of young, numbering from two to five, may be raised by one female within a year.

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